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A revision of the genus *Pseudovorticella* Foissner & Schiffmann, 1974 (Ciliophora: Peritrichida)

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Introduction

The genus *Pseudovorticella* was erected by Foissner & Schiffmann (1974) to include those peritrichs which are morphologically similar to *Vorticella* but which have a reticulate silver line system with lines running vertically as well as horizontally. The reticulate pattern of silver lines underlies a system of pellicular tubercles which covers the entire zooid surface except the disc and infundibulum.

Pellicular tubercles have been studied by several workers over the past century. Schröder (1906) showed that the tubercles of *Pseudovorticella monilata* are surface features, the distribution of which corresponds to that of the underlying striations. Ultrastructural studies by TEM (Kawamura, 1973) and SEM (Carey & Warren, 1983) have confirmed this observation. Kawamura (1973) also showed that each tubercle of *P. monilata* is a semisphere, about 2·0 μm in diameter, and contains a sphere of electron dense material. Further investigations using histochemical staining (Fauré-Fremiet & Thaureaux, 1944; Pratt & Rosen, 1983) and microanalysis (Pratt & Rosen, 1983) indicate that the tubercles contain paraglycogen. The function of the tubercles is not known although it has been suggested that they may aid predator avoidance (Spoon, 1975).

Foissner & Schiffmann (1974) noted that the silver line system is particularly useful for species diagnosis in *Pseudovorticella,* and biometric analyses have been carried out on several species (Foissner & Schiffmann, 1974 & 1975; Foissner, 1979). Parameters which are of particular taxonomic value include the total number of silver lines per zooid and dimensions of the grids formed by the intersecting vertical and horizontal lines. Morphological features traditionally used in vorticellid taxonomy are also useful diagnostic characters for the species of *Pseudovorticella*; these include the size and shape of the zooid, the number and position(s) of the contractile vacuole(s) and the shape and position of the macronucleus (Noland & Finley, 1931; Foissner, 1979; Warren, 1986).

Sixteen species of *Pseudovorticella* are recognised, twelve of which originally belonged to the genus *Vorticella*. A key to their identification is provided.

Systematics

In the scheme adopted by the Committee on Systematics and Evolution of the Society of Protozoologists (Levine *et al.,* 1980), the taxonomic position of the genus *Pseudovorticella* was given as follows:

Phylum:	Ciliophora Doflein, 1901
Class:	Oligohymenophora de Puytorac *et al.,* 1974
Subclass:	Peritrichia Stein, 1859
Order:	Peritrichida Stein, 1859
Suborder:	Sessilina Kahl, 1933
Family:	Vorticellidae Ehrenberg, 1838
Genus:	*Pseudovorticella* Foissner & Schiffmann, 1974

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Diagnosis

Solitary bell-shaped zooids borne upon a spirally contractile stalk. In all respects save one, the body and stalk of *Pseudovorticella* resemble those of *Vorticella* from which it cannot be differentiated until impregnated with silver, which reveals a reticulate silver line pattern quite unlike that of *Vorticella* (see Warren, 1986). In addition to *Vorticella* this genus could be mistaken for *Haplocaulis* in which the stalk contracts in a zigzag rather than a helical manner.

Key to the species of *Pseudovorticella*

1	With endosymbiotic zoochlorellae	2
—	Without endosymbiotic zoochlorellae	3
2	Zooid about 40 µm long; macronucleus C-shaped	***P. zooanthelligera*** (Fig. 9b)
—	Zooid 75–95 µm long; macronucleus J-shaped	***P. chlorelligera*** (Fig. 1a)
3	Diameter of peristomial lip less than or equal to maximum body width	4
—	Diameter of peristomial lip greater than maximum body width	10
4	Diameter of peristomial lip less than maximum body width	5
—	Diameter of peristomial lip equal to maximum body width	6
5	Macronucleus J-shaped	***P. difficilis*** (Fig. 1 c & d)
—	Macronucleus C-shaped	***P. papillata*** (Fig. 5c)
6	Body length less than × 2 maximum body width	7
—	Body length at least × 2 maximum body width	***P. micata*** (Fig. 2b)
7	One contractile vacuole	8
—	Two contractile vacuoles	***P. sphagni*** (Fig. 7b)
8	Macronucleus lies vertical with respect to major axis of zooid	9
—	Macronucleus lies horizontal with respect to major axis of zooid	***P. stilleri*** (Fig. 9a)
9	Zooid 65–80 µm long and with 44–54 transverse striations	***P. quadrata*** (Fig. 7a)
—	Zooid 35–45 µm long and with 20–33 transverse striations	***P. sauwaldensis*** (Fig. 8)
10	Zooid with two contractile vacuoles	11
—	Zooid with one contractile vacuole	13
11	Zooid with centrally located constriction; scopular region rounded	***P. margaritata*** (Fig. 2a)
—	Zooid without centrally located constriction; scopular region tapers towards stalk	12
12	Zooid 40–45 µm long; stalk length × 16–18 zooid length	***P. mollis*** (Fig. 3a)
—	Zooid 60–70 µm long; stalk × 3 zooid length	***P. monilata*** (Fig. 3b, c & d)
13	Diameter of peristomial lip less than body length	14
—	Diameter of peristomial lip greater than body length	***P. punctata*** (Fig. 6)
14	Zooid less than × 3 maximum body width	15
—	Zooid length greater than × 3 maximum body width	***P. mutans*** (Fig. 4 c & d)
15	Zooid 50–70 µm long × 22–48 µm wide; typically marine	***P. nebulifera*** (Fig. 4 a & b)
—	Zooid 32–50 µm long × 20 µm wide; typically freshwater	***P. pseudocampanula*** (Fig. 5 a & b)

Description of Species

P. chlorelligera (Kahl, 1935) Jankowski, 1976

V. margaritata f. *chlorelligera* Kahl, 1935
P. margaritata f. *chlorelligera* (Kahl, 1935) Foissner & Schiffmann, 1975

DIAGNOSIS (Fig. 1a & b). Zooid inverted bell-shaped, 78–95 µm long × 50 µm wide; peristomial lip 80 µm diameter; infundibulum reaches half body length; macronucleus J-shaped; numerous endosymbiotic zoochlorellae present in cytoplasm; zooid has a total of 33–53 (mean 47·7) transverse striations; grid size

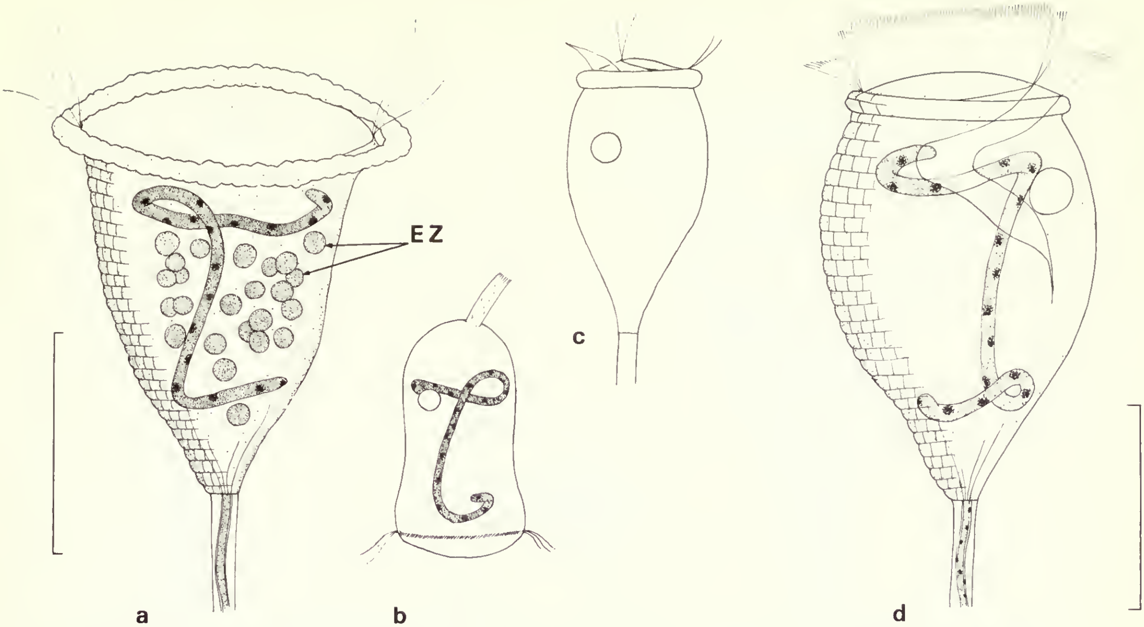

Fig. 1. (a) *P. chlorelligera* zooid, bar = 50 µm; (b) telotroch, bar = 25 µm (after Foissner & Schiffmann, 1975); (c) *P. difficilis* (after Kahl, 1935); (d) *P. difficilis*, bar = 50 µm (after Foissner & Schiffmann, 1975; called *P. difficilis* var. *magnistriata*).

1·3–3·2 µm × 2·0–4·5 µm; zooid surface with 15–28 (mean 22) pellicular pores per 100 µm^2; telotroch nearly cylindrical in shape and with a prominent epistomial membrane (Fig. 1b).

Habitat. Freshwater.

P. difficilis (Kahl, 1933) Jankowski, 1976

V. difficilis Kahl, 1933
P. difficilis var. *magnistriata* Foissner & Schiffmann, 1974

Diagnosis (Fig. 1c & d). Zooid 60–140 µm long × 40–70 µm wide; diameter of peristomial lip less than maximum body width; infundibulum reaches half body length; single contractile vacuole situated in upper part of zooid close to infundibulum; macronucleus J-shaped; 39–49 (mean 43·9) transverse striations per zooid; grid size 3·1–4·7 µm × 2·7–3·4 µm; spasmoneme with numerous thecoplasmic granules.

Habitat. Freshwater or marine.

P. margaritata (Fromentel, 1874) Jankowski, 1976

Diagnosis (Fig. 2a). Zooid inverted bell-shaped, 59–70 µm long × 50 µm wide, with a slight constriction in the central region and rounded at the scopular end; peristomial lip 70 µm in diameter; two contractile vacuoles situated in anterior part of zooid; macronucleus C-shaped and situated in centre of zooid.

Habitat. Freshwater, particularly eutrophic lakes and stagnant water.

Remarks. This species has been redescribed by Kahl (1935) and Stiller (1971).

P. micata (Kahl, 1933) nov. comb.

V. micata Kahl, 1933

Diagnosis (Fig. 2b). Zooid elongate, 65 µm long × 25 µm wide; peristomial lip 25 µm in diameter; disc flat and slightly elevated above peristome; infundibulum reaches one third zooid length; contractile vacuole situated in upper part of zooid close to infundibulum.

Habitat. Marine.

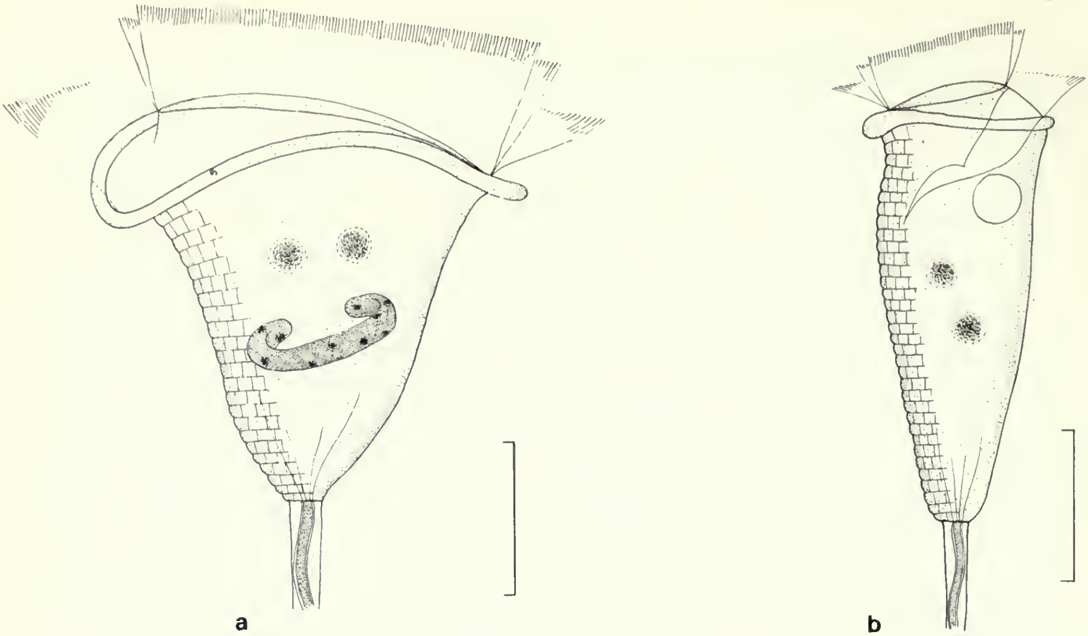

Fig. 2. (a) *P. margaritata* , bar = 25 µm (composite from Kahl, 1935 and Stiller, 1971); (b) *P. micata*, bar = 25 µm (after Kahl, 1935).

P. mollis (Stokes, 1887) nov. comb.

V. mollis Stokes, 1887

DIAGNOSIS (Fig. 3a). Zooid inverted bell-shaped, 40–45 µm long × 25 µm wide; peristomial lip 40 µm in diameter; infundibulum reaches one third body length; two contractile vacuoles situated in anterior part of zooid; stalk × 16–18 zooid length.

HABITAT. Freshwater

REMARKS. Although this species was not drawn by Stokes (1887), it has been observed and figured by Nenninger (1948).

P. monilata (Tatem, 1870) Foissner & Schiffmann, 1974

V. lockwoodii Stokes 1884
V. monilata Tatem, 1870

DIAGNOSIS (Fig. 3b, c & d). Zooid inverted bell-shaped, 45–70 µm long × 40–45 µm wide; peristomial lip 50 µm in diameter; infundibulum reaches half body length; two contractile vacuoles situated in anterior part of zooid; macronucleus J-shaped; 31–41 (mean 35·3) transverse striations per zooid; grid size 2·5–3·5 µm × 1·5–2·5 µm; stalk × 3 body length; spasmoneme with thecoplasmic granules; telotroch cone-shaped with prominent epistomial membrane.

HABITAT. Freshwater, often forming pseudocolonies; Pratt & Rosen (1983) reported large numbers of *Pseudovorticella (Vorticella) monilata* attached the Cyanobacterium *Anabaena flos-aquae*.

P. mutans (Penard, 1922) Foissner, 1979

V. mutans Penard, 1922

DIAGNOSIS (Fig. 4c & d). Zooid inverted bell-shaped, 65–95 µm long × 18–25 µm wide; peristomial lip 25 µm in diameter; disc convex; infundibulum reaches half body length; contractile vacuole situated in upper half of body close to infundibulum; macronucleus J-shaped; zooid has 40–47 (mean 43) transverse striations; grid

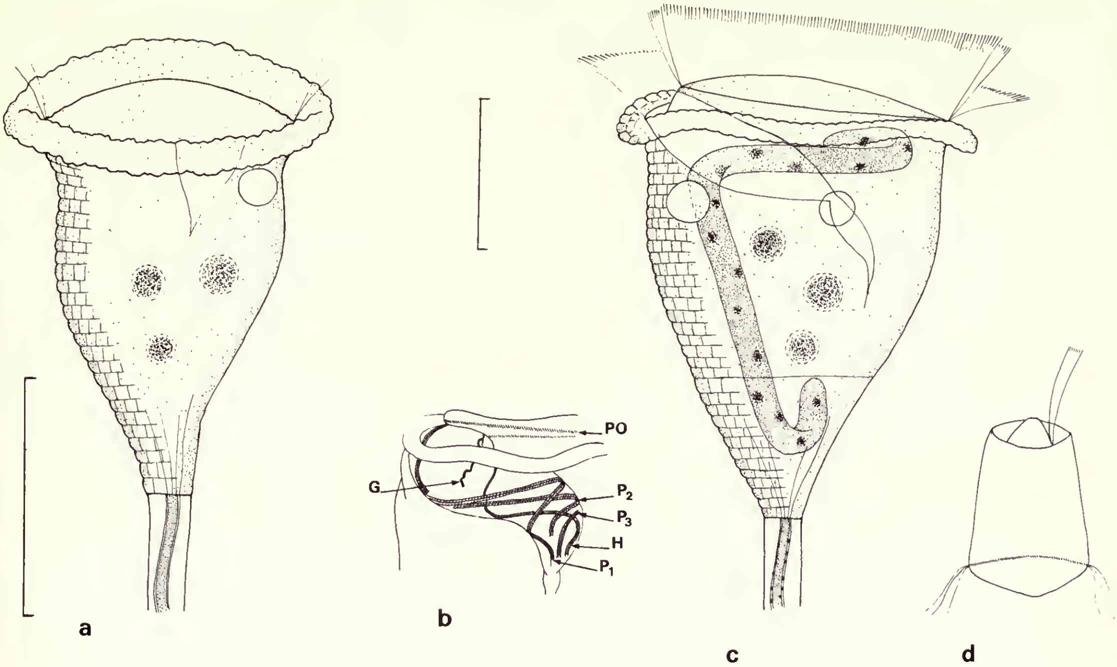

Fig. 3. (a) *P. mollis,* bar = 25 µm (after Nenninger, 1948); (b) *P. monilata* showing oral ciliation (detail from Pätsch, 1974); (c) zooid, bar = 25 µm; (d) telotroch (after Foissner, 1979). G = germinal kinety; H = haplokinety; P_1, P_2, P_3 = 1, 2, 3, peniculus; PO = polykinety.

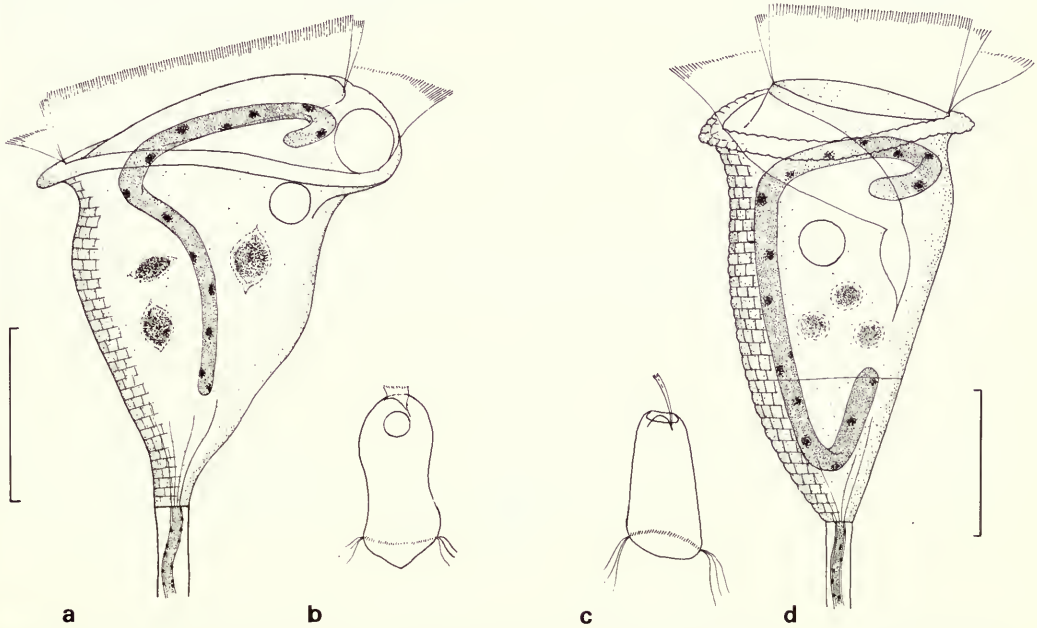

Fig. 4. (a) *P. nebulifera* zooid, bar = 25 µm (after Noland & Finley, 1931); (b) telotroch (after Barlow & Finley, 1976b); (c) *P. mutans* telotroch; (d) zooid, bar = 25 µm (after Foissner, 1979).

size 1·4–1·5 µm × 1·5–2·2 µm; stalk ×5 body length and 8·0 µm wide; spasmoneme with thecoplasmic granules; telotroch with prominent epistomial membrane.

HABITAT. Freshwater.

P. nebulifera (Müller, 1786) Jankowski, 1976

V. nebulifera Müller, 1786

DIAGNOSIS (Fig. 4a & b). Zooid inverted bell-shaped, 38–78 µm (mean 60 µm) long × 22–48 µm (mean 37 µm) wide; slightly constricted beneath peristomial lip which measures 32–66 µm (mean 53 µm) in diameter; single contractile vacuole situated close to infundibulum; macronucleus J-shaped; stalk 50–800 µm (mean 150 µm) long × 3·5–6·0 µm (mean 4·7 µm) wide; spasmoneme with thecoplasmic granules; telotroch 47–75 µm (mean 60 µm) long; cyst 37 µm in diameter.

HABITAT. Marine or freshwater.

REMARKS. Redescribed by Noland & Finley (1931); for telotroch and SEM studies, see Barlow & Finley (1976a & b).

P. papillata (Stiller) Jankowski, 1976

V. microstoma f. *monilata* Stiller (see Stiller, 1971)

DIAGNOSIS (Fig. 5c). Zooid 35–80 µm (mean 55 µm) long × 22–50 µm (mean 35 µm) wide, the maximum body width being the mid region of the zooid; peristomial lip 12–25 µm (mean 23 µm) in diameter; disc convex; infundibulum reaches one third body length; contractile vacuole situated in anterior part of zooid; macronucleus C-shaped and lies longitudinally with respect to major axis of zooid.

HABITAT. Freshwater, particularly under conditions of high biochemical oxygen demand (BOD_5).

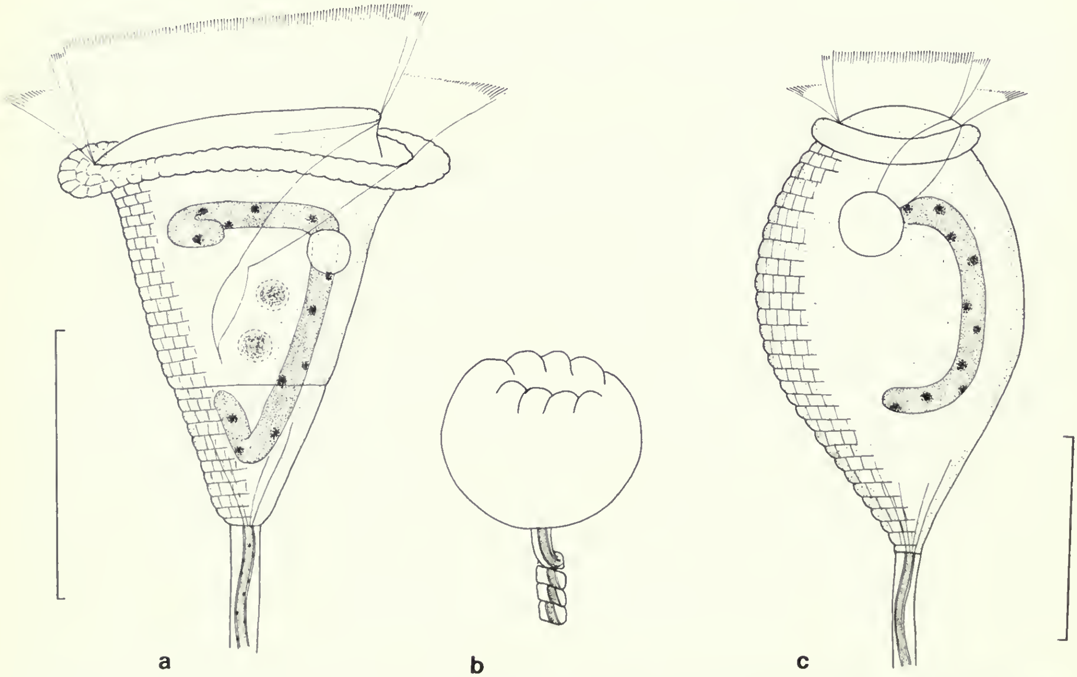

Fig. 5. (a) *P. pseudocampanula* relaxed zooid, bar = 25 µm; (b) contracted zooid (after Foissner, 1979); (c) *P. papillata*, bar = 25 µm (after Stiller, 1971).

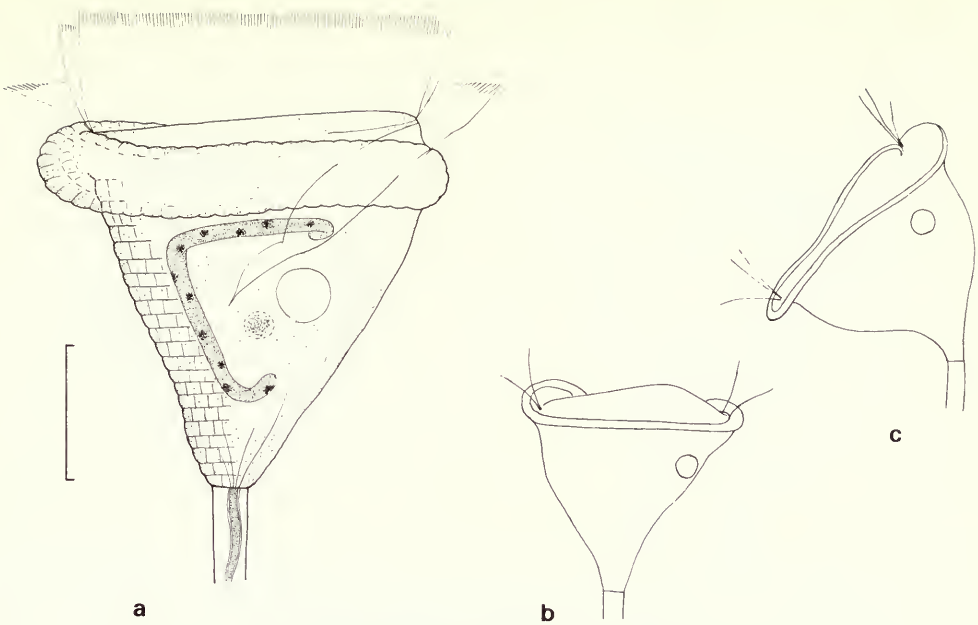

Fig. 6. *P. punctata,* (a) bar = 25 µm (after Dons, 1918); (b) after Stiller (1946) (called *Vorticella subconica*); (c) after Kahl (1935) (called *Vorticella perlata*).

P. pseudocampanula Foissner, 1979

Diagnosis (Fig. 5a & b). Zooid conical/inverted bell-shaped, 32–50 µm (mean 40 µm) long × 20 µm wide; peristomial lip 35 µm in diameter; upon contraction, peristomial lip becomes puckered (Fig. 5b); infundibulum reaches half body length; contractile vacuole situated close to infundibulum; macronucleus J-shaped; zooid has 44–51 (mean 46·6) transverse striations; grid size 1·3–2·6 µm × 1·5–3·0 µm; stalk × 7 body length; thecoplasmic granules present on spasmoneme.

Habitat. Freshwater.

P. punctata (Dons 1918) nov. comb.

V. punctata Dons, 1918
V. subconica Stiller, 1946
P. subconica (Stiller, 1946) Jankowski, 1976

Diagnosis (Fig. 6). Zooid conical or inverted bell-shaped, 40–50 µm long × 40 µm wide; peristomial lip 50–55 µm in diameter; disc convex; infundibulum reaches one third body length; contractile vacuole situated in upper part of zooid; macronucleus J-shaped; stalk × 4–5 body length and 4·0 µm wide.

Habitat. Marine.

P. quadrata Foissner, 1979

Diagnosis (Fig. 7a). Zooid 65–80 µm (mean 70 µm) long × 55 µm wide; peristomial lip 60 µm in diameter; infundibulum reaches half body length; contractile vacuole situated in anterior part of zooid; macronucleus J-shaped; zooid has 44–54 (mean 48·3) transverse striations; grid size 1·5–2·8 µm × 1·3 × 2·7 µm; stalk × 7 body length and 9·0 µm wide; spasmoneme with thecoplasmic granules.

Habitat. Freshwater.

P. sauwaldensis Foissner & Schiffmann, 1979

Diagnosis (Fig. 8). Zooid shape variable, usually inverted bell-shaped 35–45 µm long × 20 µm wide; peristomial lip 20 µm in diameter and 3·0 µm thick; disc convex; infundibulum reaches half body length;

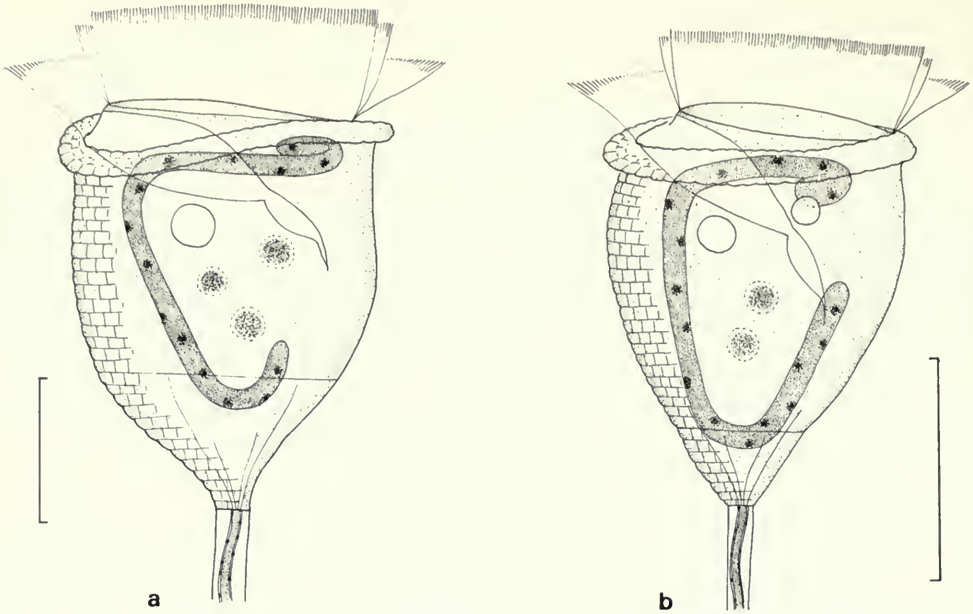

Fig. 7. (a) *P. quadrata*, bar = 25 µm; (b) *P. sphagni*, bar = 25 µm (after Foissner, 1979).

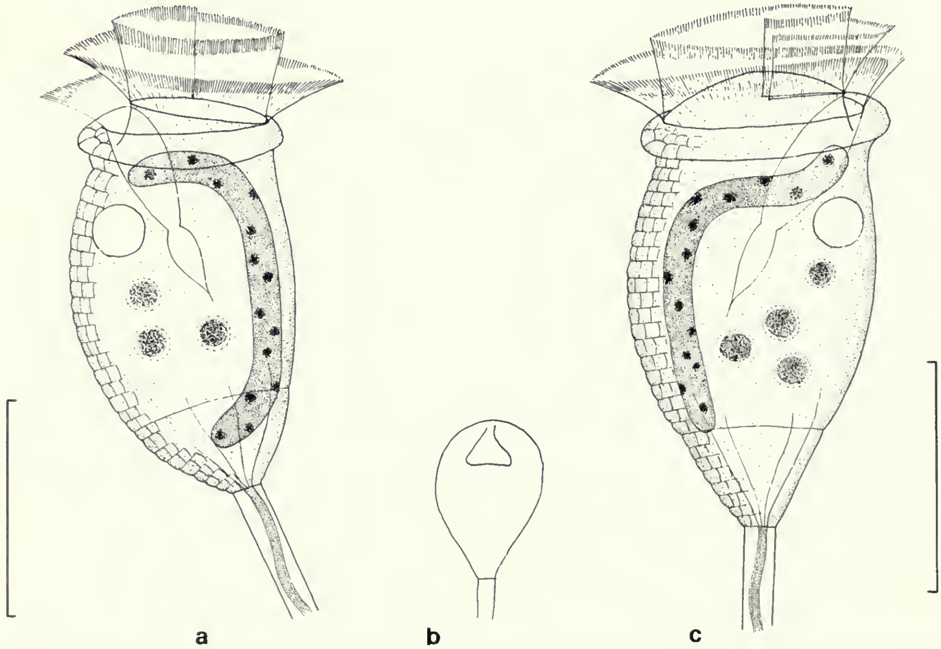

Fig. 8. *P. sauwaldensis* (a) normal zooid, bar = 20 µm; (b) contracted zooid; (c) showing variability of macronucleus and zooid shape, bar = 20 µm (after Foissner & Schiffmann, 1979).

contractile vacuole situated in upper part of zooid close to infundibulum; macronucleus vermiform, variable in shape and situated longitudinally with respect to major body axis; pellicle has 20–33 (mean 29) transverse striations; grid size 0·9–1·5 µm × 0·7–2·5 µm; stalk × 1–3 body length.

HABITAT. Freshwater.

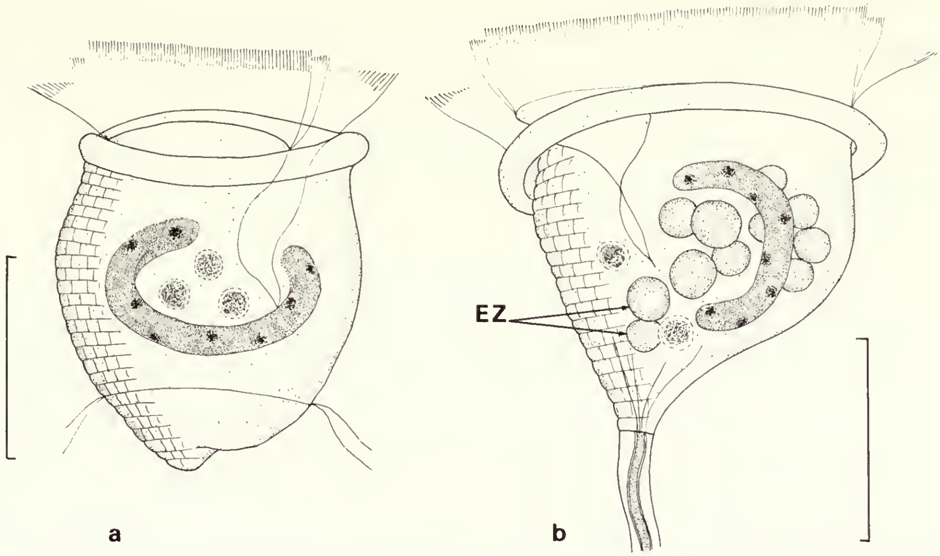

Fig. 9. (a) *P. stilleri*, bar = 50 µm (after Stiller, 1963); (b) *P. zooanthelligera*, bar = 25 µm (after Stiller, 1968). EZ = endosymbiotic zoochlorellae.

P. sphagni Foissner, 1979

Diagnosis (Fig. 7b). Zooid inverted bell-shaped, 40–50 µm long × 30 µm wide; peristomial lip 30 µm in diameter; infundibulum reaches one third body length; two contractile vacuoles situated in anterior part of zooid; macronucleus J-shaped with elongate distal arm; zooid has 34–37 (mean 35·5) transverse striations; grid size 1·6–1·9 µm × 2·5–2·7 µm.

Habitat. Freshwater, originally isolated from *Sphagnum* bogs.

P. stilleri n. sp.

V. campanula f. *monilata* Stiller, 1963

Diagnosis (Fig. 9a). Zooid inverted bell-shaped, 85 µm long × 80 µm wide; peristomial lip 80 µm in diameter; infundibulum reaches half body length; macronucleus C-shaped and lies horizontally across centre of zooid.

Habitat. Freshwater, attached to the duckweed *Lemna minor*.

P. zooanthelligera (Stiller, 1968) nov. comb.

V. zooanthelligera Stiller, 1968

Diagnosis (Fig. 9b). Zooid inverted bell-shaped, 40–42 µm long × 40 µm wide; peristomial lip 50 µm in diameter; disc flat; infundibulum reaches one third body length; macronucleus C-shaped and lies longitudinally in zooid; cytoplasm contains numerous endosymbiotic zoochlorellae; stalk × 5 body length.

Habitat. Freshwater.

Incertae sedis

Pseudovorticella sp. (Graham & Graham, 1978) nov. comb.

Vorticella sp. Graham & Graham, 1978

Graham & Graham (1978) made an ultrastructural study of a vorticellid (*Vorticella* sp.) furnished with pellicular tubercles and containing endosymbiotic zoochlorellae. The presence of pellicular tubercles suggests that this organism should belong to the genus *Pseudovorticella*. However other important diagnostic features, for example the macronucleus, contractile vacuole(s) and shape of the relaxed zooid, were not recorded. Only when such data is available will it be possible to determine the exact status of this organism.

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I would like to thank Dr W. Foissner for his helpful criticism of the manuscript.

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Index

Index of extant species; annotated list of nominal species.

P. anabaenae (Stiller, 1940) Jankowski, 1976 was transferred to the genus *Haplocaulis* by Stiller (1971).
P. chlorelligera (Kahl, 1935) Jankowski, 1976 2
P. chlamydophora (Penard, 1922) Jankowski, 1976 = *Vorticella vestita* Stokes, 1883 (see Warren, 1986).
P. difficilis (Kahl, 1933) Jankowski, 1976 3
P. difficilis var. *magnistriata* Foissner & Schiffmann, 1974 = *P. difficilis*.
P. lima (Kahl, 1935) Jankowski, 1976. This species appears to have pellicular granules rather than tubercles; it should therefore remain in the genus *Vorticella (V. lima)* until it has been redescribed.
P. margaritata (Fromentel, 1874) Jankowski, 1976 3
P. micata (Kahl, 1933) nov. comb. 3
P. mollis (Stokes, 1887) nov. comb. 4
P. monilata (Tatem, 1870) Foissner & Schiffmann, 1974 4
P. mutans (Penard, 1922) Jankowski, 1976 4
P. nebulifera (Müller, 1786) Jankowski, 1976 6
P. papillata (Stiller) Jankowski, 1976 6
P. pelagica (Gajewskaja, 1933) Jankowski, 1976 was transferred to the genus *Haplocaulis* by Stiller (1971).

P. perlata (Kahl, 1933) Jankowski, 1976 = *P. punctata*.

P. plicata (Gourret & Roeser, 1886) Jankowski, 1976 appears to be identical to *Vorticella elongata* Fromentel, 1874 (Warren, 1986).

P. pseudocampanula Foissner, 1979 7

P. punctata (Dons, 1918) nov. comb.. 7

P. quadrata Foissner, 1979 7

P. sauwaldensis Foissner & Schiffmann, 1979 7

P. sphagni Foissner, 1979 9

P. stilleri (Stiller, 1963) n. sp. 9

P. subconica (Stiller, 1946) Jankowski, 1976 appears to be identical to *P. punctata*.

P. vestita (Stokes, 1883) Jankowski, 1976. A membranous alveolar covering overlays the pellicle of this species. There is, however, no evidence of pellicular tubercles or of an underlying reticulate pattern of silver lines. This species should therefore remain in the genus *Vorticella (V. vestita)* until it has been redescribed.

P. voeltzkowi (Sondheim, 1929) Jankowski, 1976. This species has spine-like projections on its pellicle. There is, however, no evidence that it has either pellicular tubercles or a reticulate pattern of silver lines. It should therefore remain in the genus *Vorticella (V. voeltzkowi)* until a redescription is available.

P. zooanthelligera (Stiller, 1968) nov. comb. 9

The taxonomic status of the genera *Pontigulasia*, *Lagenodifflugia* and *Zivkovicia* (Rhizopoda: Difflugiidae)

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Introduction

The significance of the different structural elements utilised to provide an internal dividing wall in the shell of the genus *Pontigulasia* Rhumbler, 1896 was employed by Ogden (1983) to divide the genus into two, with the creation of a new genus *Zivkovicia* Ogden, 1983. At the same time a new genus *Lagenodifflugia* was erected by Medioli & Scott (1983) to accommodate *Difflugia vas* Leidy, 1874, a species that he (Leidy, 1879) later redescribed as a variety of *Difflugia pyriformis*. Medioli & Scott (1983) considered their new genus to be distinct from species of *Difflugia* because the shell was divided into a bulbous main part and a neck, the two parts being separated by an internal diaphragm pierced by a single, central, usually large orifice. In the same work Medioli & Scott redefined the genus *Pontigulasia*, describing the main characters as a constriction of the neck marking the position where a perforated internal diaphragm often extends across this region, and at times a bent neck combined with the internal restriction simulating a spiral arrangement. They also stated that the diaphragm is seldom present in fossilised forms. The amendment of the diagnosis to contain a 'bent neck' was made to allow Medioli & Scott to include some '*Lecquereusia*-like' specimens in their description of *Pontigulasia compressa*, and to suggest the possibility of combining the genera *Lesquereusia* and *Pontigulasia*, the former being the senior synonym.

I am most grateful to Dr Drew Haman and Dr Georges Merinfeld for directing my attention to the nomenclature problems posed by the creation of these two new genera. The present report is an attempt to clarify the status and diagnosis of the three genera *Pontigulasia*, *Lagenodifflugia* and *Zivkovicia*.

Taxonomy

The taxonomic problem caused by the creation of two new genera relates to the interpretation and validity of the structures and openings found associated with the inner dividing wall. There are only a few descriptions and figures of these features around which the diagnoses have been erected. One reason for this is the difficulty of trying to see inside the shell either *en face* or laterally due mainly to the opacity of the mineral particles of which it is constructed. Several techniques have been tried to overcome this, for example immersion in clove oil or canada balsam and demineralisation by hydrofluoric acid. Modern techniques have now obviated this problem and allow a new appraisal of this feature (Ogden, 1983).

Each genus will be reassessed here on the basis of the available descriptions and the author's earlier observations.

Pontigulasia Rhumbler, 1896

The first author to recognise the inner dividing wall was Rhumbler (1896) who erected the genus *Pontigulasia* using this feature as a major diagnostic character to separate it from *Difflugia*, and described and clearly figured it as an internal 'schlundbrücke'-throat bridge. He described three

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new species belonging to this genus, *P. compressa, P. incisa* and *P. spiralis*. Since then Hopkinson (1919) has redescribed *P. compressa* under a new name *P. rhumbleri,* the name *compressa* was preoccupied by Carter's (1864) species, and *P. incisa* has become a synonym of *P. elisa* (Penard, 1893), both the earlier descriptions being for species of *Difflugia*. The authoritative date for *P. rhumbleri* is considered to be Hopkinson's redescription (1919), not the note mentioned as an addition to *P. elisa* on p. 162 of Cash & Hopkinson (1909) where Hopkinson suggests that 'Rhumbler's *P. compressa* (which might now be called *P. Rhumbleri*)', his brackets. Furthermore, the date of Rhumbler's work is erroneously quoted by Cash *et al.* (1919) and Loeblich & Tappan (1964) as 1895, which is the date of presentation, whereas the publication date of the volume was 1896, as listed in Penard's (1902) bibliography.

The internal bridge has been redescribed by Ogden (1983), who examined the dividing wall *in situ* using scanning electron microscopy, and showed it to be correctly termed a bridge, as it represented a rather weak connection between the two lateral walls of the compressed shell in *P. rhumbleri*. It is often difficult to see by optical microscopy because the shells are laterally compressed, and in this the normal viewing position the bridge appears to be a dark floating band situated centrally in the neck region without any apparent connection to the shell wall. This is not surprising, because each junction of the bridge with the wall is about a sixth of the shell diameter at this point.

Although Rhumbler described three species, since that time two of these *P. incisa* and *P. spiralis* have been considered to be synonyms (Cash & Hopkinson, 1909), and it was not until Leoblich & Tappan (1964) that a type species, *P. rhumbleri,* was designated.

DIAGNOSIS. Shell pyriform, sometimes with a constriction of the neck, either circular or compressed in transverse section; composed mainly of agglutinate mineral particles with some diatom frustules or siliceous plates, bound by a network of organic cement; aperture terminal, circular; internally the shell is divided into two regions by a narrow bridge, made mainly of organic cement with some agglutinate particles, stretched between the lateral walls at about one third of the body length from the aperture. Type species *P. rhumbleri* Hopkinson, 1919, with four other species (Chardez, 1985), *P. compressoidea* Jung, 1942; *P. elisa* (Penard, 1893); *P. sarrazinensis* Chardez & Gaspar, 1984 and *P. spiralis* Rhumbler, 1896.

Lagenodifflugia Medioli & Scott, 1983

This genus was established for the single species *Difflugia vas* Leidy, 1874. After his original description Leidy later considered (1879) that this species was a variety of *Difflugia pyriformis,* from which it differed by a constriction of the neck, there was no reference to an internal structure associated with the constriction. Penard (1902) transferred this species to *Pontigulasia* and considered it to be a synonym of his new species *P. spectabilis*. It was corrected to the valid binomen *P. vas* by Schoutenden (1906), and *spectabilis* has since been considered a synonym of *vas*. As *P. vas* was described as having a similar external constriction to *spectabilis,* the assumption was that it had two openings bisecting the internal diaphragm. Notwithstanding this, Stump (1935, 1936 and 1943) in a series of experiments with specimens he initially thought were *Difflugia oblonga,* later found that in sectioned shells there was an internal division with a single opening and subsequently described them as *Pontigulasia vas*. Although Stump does not clearly state that his specimens had a single, central opening, his diagrams without exception suggest that this interpretation is correct. That the strength of the diaphragm is equal to that of the shell wall is extrapolated from his de-mineralised sections which show the continuous nature of these structures.

Using the joint reports of Leidy and Stump, a composite description of a species emerges: it sometimes has a constriction of the neck that separates the anterior third of the shell from the main body; at this point an internal diaphragm is present which is pierced by a single, central, circular opening.

Medioli & Scott (1983) do not illustrate the internal division in their specimens but describe it as a 'large orifice'. They presume that their material is conspecific with that of Leidy and Stump, possibly because all the specimens were collected in America. Fortunately, a single specimen with an internal division was found in material kindly left at the British Museum (Natural History) by F. S. Medioli and helps to confirm their presumption. The specimen had the following measurements: 174 μm long, 108 μm broad, diameter of aperture 37 μm and diameter of internal opening 27 μm. Furthermore the organic cement pattern of this specimen was typical of that illustrated earlier (Ogden, 1983).

DIAGNOSIS. Shell pyriform, often with a constriction of the neck, most frequently circular in cross-section but sometimes slightly compressed, composed mainly of agglutinate mineral particles bound by an organic cement; aperture terminal, circular; internally the shell is partitioned into two regions by a diaphragm constructed as part of the shell wall but having a single central orifice. Type species *L. vas* (Leidy, 1874). Three other species are here attributed to the genus on the basis of having a single opening in a well constructed diaphragm: *L. bryophila* (Penard, 1902) (see Ogden, 1983 for recent description of this species); *L. montana* (Ogden & Zivkovic, 1983) and *L. epiouxi* (Chardez & Gaspar, 1984).

Zivkovicia Ogden, 1987 gen. nov.

This genus was erected by Ogden (1983) to accommodate those species of *Pontigulasia* which had a diaphragm with either one or two internal openings. At that time no distinction was drawn between the number of openings in the diaphragm. With the creation of *Lagenodifflugia* to represent those specimens with a single opening, *Zivkovicia* is redefined here to represent those species with two openings.

In the earlier report (Ogden, 1983), due to an oversight, a type species for *Zivkovicia* was not designated, so under Article 13(b) of the International Code of Zoological Nomenclature the genus is not taxonomically valid. Nevertheless, the name is still available and to avoid confusion is used again here, with an amended diagnosis.

Although Carter's (1864) original description of *Diffugia compressa* did not include a mention of an internal diaphragm, his drawings are so precise that they show the typical V-shaped notch on the shell which represents the internal diaphragm. This structure is clearly illustrated by Figs 18–25 of Ogden (1983). It is therefore proposed as the type-species of the genus. The earlier discussion (p. 14) relating to the incorrect synonymy of *P. vas* and *P. spectabilis,* allows *spectabilis* to be available to include the original description of specimens with a bisected diaphragm (Penard, 1902) and the recent description by Ogden (1983), whose *P. vas* now becomes a synonym of *Z. spectabilis.*

DIAGNOSIS. Shell pyriform, often with a distinct constriction of the neck region, either circular or compressed in transverse-section, composed mainly of agglutinate mineral particles bound by an organic cement matrix; aperture terminal, usually circular; internally the shell is partitioned into two parts by an extension of the shell wall to form a diaphragm which is bisected by two circular openings. Type species *Z. compressa* (Carter, 1864), other species *Z. spectabilis* (Penard, 1902) and *Z. flexa* (Cash & Hopkinson, 1909). A recent description of the latter species can be found in Ogden (1983).

Discussion

Associated problems of clearly identifying the internal openings were discussed previously (Ogden, 1983). Suffice to say here that both these openings and the aperture can be sealed by an organic cyst membrane, and the incidence of a single specimen with a trisected diaphragm in *Z. compressa* (Fig. 28, Ogden, 1983) is considered to be an isolated deformity.

In discussing a possible relationship between *Pontigulasia* Rhumbler, 1896 and *Lesquereusia* Schlumberger, 1845, Medioli & Scott (1983) suggest that both genera are characterised by a constriction at the base of the neck which corresponds to an internal diaphragm, and further state that a morphological intergradation exists between the two genera. They consider that the remaining difference between the genera, that *Lesquereusia* is constructed of siliceous idiosomes whereas *Pontigulasia* is always reported to be composed of xenosomes, is insufficient to separate these two genera.

It has already been established by Stump (1936, 1943) that *P. vas* would not construct a shell or reproduce in the absence of extraneous material, even in the presence of abundant food, and that such deprived animals commenced normal reproductive activities when shell making material was reintroduced. He concluded that *P. vas* was unable to secrete its own shell material and suggested a possible alternative that individuals might be produced without a shell covering. No reports of such naked individuals have been recorded in the literature, but it is well known that some agglutinate species are capable of constructing an organic shell, identical to that which in the field incorporates mineral particles (Hedley *et al.,* 1976; Netzel, 1972, 1976). Furthermore, the deposition of siliceous structures by *Lesquereusia spiralis* are carried out in the cytoplasm of the animal (Harrison *et al.,* 1981), and this species is capable of constructing a shell in the absence of extraneous material. It is equally capable of incorporating xenosomes and Stump used this ability for creating 'windows' to observe cytoplasmic activity. A new family the Lesquereusiidae was designated (Ogden, 1979) to include those members of the Lobosia which secrete their own siliceous elements, e.g. *Lesquereusia, Netzelia* Ogden, 1979, and *Quadrulella* Cockerell, 1909.

The suggestion by Medioli & Scott (1983) of considering a relationship between *Lesquereusia* and *Pontigulasia* is perhaps best treated as an indiscretion on the part of geologists venturing into the alien field of biology. Phylogenetic interpretations should be based on the animal as a complete organism, which in protozoa would include information on cytoplasmic detail, movement, reproduction as well as external coverings, especially when such information exists in publication and the animals are easily collected from the field.

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Since this manuscript was submitted for publication the author has become aware of a paper by Medioli & Scott (1985), in which they have designated type specimens for certain species. In dealing with species of *Pontigulasia, Lagenodifflugia* and *Zivkovicia* they make assumptions based solely on published descriptions and micrographs of fossil specimens, which do not have information relating to the main diagnostic feature the internal dividing diaphragm. In their original paper (Medioli & Scott, 1983), they comment on never having been able to satisfactorily observe the diaphragm of *P. compressa* (Carter, 1864), and their failure is again reiterated in Medioli & Scott (1985), As neither their figures nor plates illustrate an internal structure it suggests that they have failed by both optical and electron microscopy to see this feature in any of their specimens. They presume the presence of a diaphragm solely on it corresponding in position to the external constriction. Although they admit that this external constriction is often obscured by agglutinate material.

Furthermore, the specimen they selected as neotype of *L. vas,* from their Maritime Canada sample does not even resemble the original selected figure from Leidy (1879). In fact they chose an example which was intermediate between Leidy's figured specimen, a smoothly agglutinate form, and their extreme cases of coarse agglutination.

Both of Medioli & Scott's (1983, 1985) papers concerning these genera must be of minimal value because of their failure to describe or identify the internal structures which typify these genera. Its absence suggests that they have been examining species of *Difflugia.* Their insistance that the diaphragm is absent in fossil forms (p. 35, 1983; p. 29, 1985) of *Pontigulasia compressa* (Carter, 1864) would indicate that they are dealing with species of *Difflugia.* The construction of the diaphragm in this species (Ogden, 1983) is so robust, being continuous and as thick as the shell wall, that even in fractured shells it is the wall that breaks and not the diaphragm. Although often by convenience such breaks occur at the junction of the wall and diaphragm. Notwithstanding this, specimens clearly identified as *Zivkovicia compressa* (Carter, 1864) have been recovered from core samples taken in Lake Ullswater which had complete diaphragms (Ogden & Ellison, in prep.), and in addition possessed the typical organic cement units, described by Ogden (1983), specific to this genus.

Medioli, F. S. & Scott, D. B. 1985. Designation of types, for one genus and nine species of Arcellaceans (Thecamoebians), with additional original reference material for four other species. *Journal of Foraminiferal Research* **15:** 24–37.

A revision of the foraminiferal genus *Adercotryma* Loeblich & Tappan, with a description of *A. wrighti* sp. nov. from British waters

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Adercotryma Loeblich & Tappan (1952) was erected to accommodate *Lituola glomerata* Brady (1878), a species assigned subsequently to *Haplophragmium, Haplophragmoides* and *Trochammina* by various authors. A recent examination of the type material in the British Museum (Natural History), and of specimens from other collections deposited there and in the National Museum of Ireland, led to the discovery that the original definition was inadequate and to the recognition of a second species. The purpose of this paper is to emend the diagnosis of *Adercotryma,* to redescribe *A. glomeratum* (Brady), and to describe the new species.

The generic diagnosis below is based on the redescription of the type species, and differs from the original definition in that it recognises the significance of the asymmetrically placed aperture and shows the coiling to be trochospiral. *Adercotryma* is therefore transferred from the Lituolacea to the Trochamminacea and placed in a new subfamily of the Trochamminidae. The definition follows the format adopted by Brönnimann *et al.* (1983) in their reclassification of the Trochamminacea.

Superfamily **TROCHAMMINACEA** Schwager, 1877
Family **TROCHAMMINIDAE** Schwager, 1877
Subfamily **ADERCOTRYMINAE** nov.

DEFINITION. Test free; adult, a completely or almost completely involute, cone-like, trochospire; wall agglutinated, imperforate, single-layered, aperture interiomarginal, single; without secondary septa or infoldings of the umbilical chamber walls or incomplete secondary partitions.

TYPE GENUS. *Adercotryma* Loeblich & Tappan, 1952.

REMARKS. The Adercotryminae differs from all other subfamilies in that its members are completely or almost completely involute on the spiral side. Brönnimann *et al.* (1983: 204) distinguished the Trochamminacea from the Ataxophragmiacea on the ratio of spire height to umbilical diameter: the former being always smaller than the latter in the Trochamminacea. At first sight, the high cone-shaped test of *Adercotryma* does not fulfil this criterion, but since the coiling is involute and the proloculus is situated within the shell (see Figs 3, 6), the spire height measured from the proloculus is invariably less than the umbilical diameter.

Genus *ADERCOTRYMA* Loeblich & Tappan, 1952

TYPE SPECIES. *Lituola glomerata* Brady, 1878. Recent, marine; distribution apparently worldwide. Lectotype from Arctic waters.

EMENDED DEFINITION. Test free; coiling trochospiral, adult an inverted cone, completely or almost completely involute on both sides. Chambers axially elongate. Aperture single, interiomarginal, umbilical, symmetrical with respect to long axis of chamber. Wall agglutinated, single layered, imperforate.

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REMARKS. The slit-like aperture rests with its border on the first and on the penultimate chamber of the final whorl (*Paratrochammina*-type aperture). *Adercotryma* differs from *Paratrochammina* Brönnimann, 1979 (type species: *P. madierae* Brönnimann, 1979) and all other genera of the Trochammininae by its spirally involute enrolment, axially elongate chambers, symmetrical interiomarginal aperture (with respect to the long axis of the chamber), and inverted cone-like test.

Adercotryma glomeratum (Brady)
Figs 1, 2A–F, 3A, 4A–E, 5A–J, 6A–F

1878 *Lituola glomerata* Brady: 433, pl. 20, figs 1a–c.
1884 *Haplophragmium glomeratum* (Brady); Brady: 309, pl. 34, figs 15–18.
1910 *Haplophragmoides glomeratum* (Brady) (*sic*); Cushman: 104, figs 158–161 (after Brady, 1884).
1931 *Trochammina glomerata* (Brady); Wiesner: 112, pl. 17, figs 204, 205.
1952 *Adercotryma glomerata* (Brady) (*sic*); Loeblich & Tappan: 141, figs 1–4.
1961 *Adercotryma glomerata glomerata* (Brady); Saidova: 35, pl. 10, fig. 54.
1961 *Adercotryma glomerata abyssorum* Saidova (*sic*): 36, pl. 10, fig. 55.
1975 *Adercotryma glomerata antarctica* Saidova (*sic*): 75, pl. 96, fig. 6.

MATERIAL. Extant material in the Brady Collection of the British North Polar Expedition (1875–1876), labelled *Lituola glomerata*, is as follows: Station A, off Tyndall Glacier, 27 fms (49 m); F, between Walrus Shoal and Victoria Head, 57 fms (104 m); H, Franklin Pierce Bay, 13–15 fms (24–28 m); I, Allman Bay, 25 fms (46 m); J, Dobbin Bay, 45–47 fms (82–86 m); K, Dobbin Bay, 113 fms (207 m); N, off Hayes Point, 35 fms (64 m); O, off Cape Frazer, 50 fms (92 m) and P, off Cape Frazer, 80 fms (146 m). These localities are from the northern part of Baffin Bay and Smith Sound (between Ellesmere Island, NE Canada, and W Greenland). All the slides contain a few specimens at least, and some (e.g. station G) as many as 50.

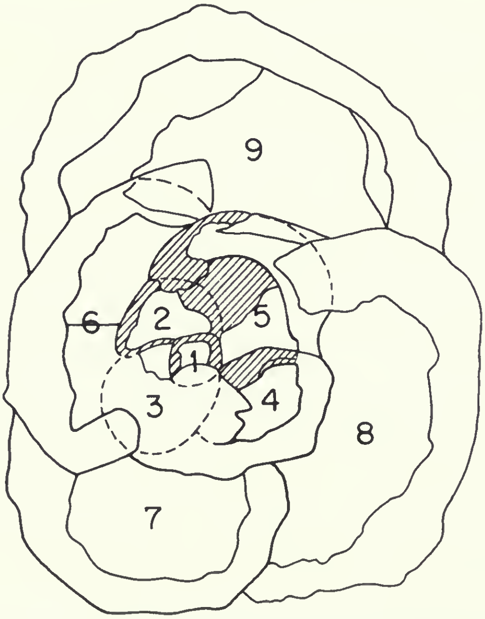


Fig. 1. *Adercotryma glomeratum* (Brady). Paralectotype, 1955.10.28.1732. Interpretative drawing of specimen in Figs 6A–C, taken at the third level of dissection (see explanation of Fig. 6C), showing chambers 1 to 9. Hatched areas represent exposed walls of earliest chambers. × 300.

From Franklin Pierce Bay, lat. 79°28′N, station H, depth 46 fathoms (84 m). British North Polar Expedition of 1875–1876, ex BMNH slide no. 1955.10.28.1731–1780, labelled *'Lituola glomerata* Brady'.

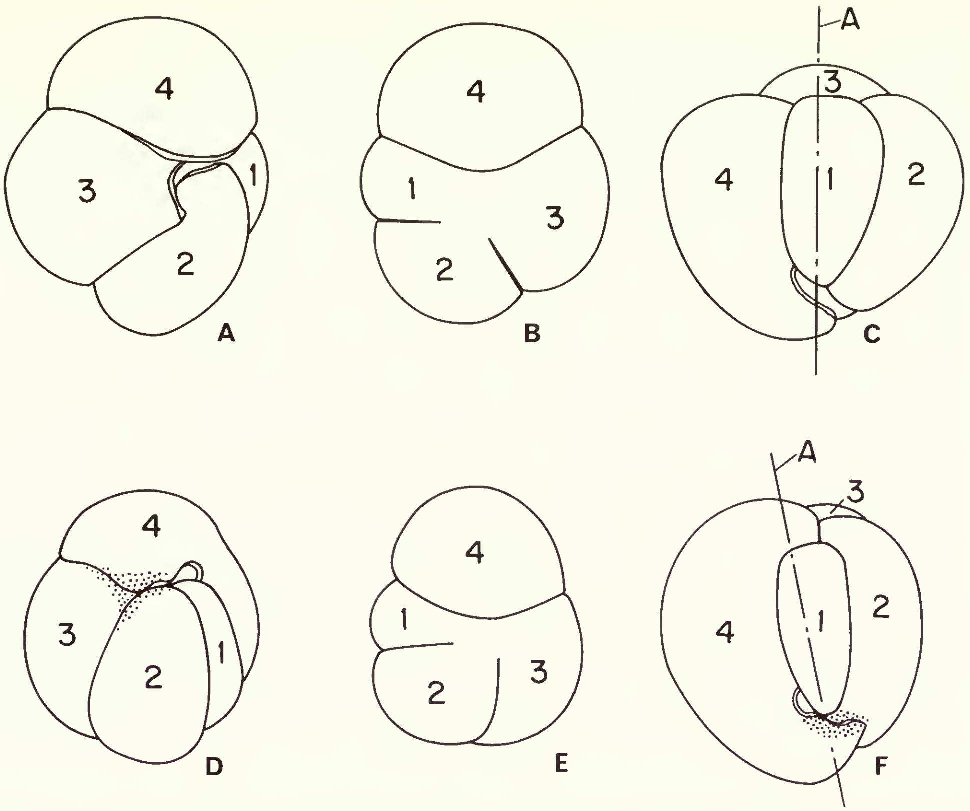


Fig. 2A–F. *Adercotryma glomeratum* (Brady). 2A–C, Paralectotype, 1955.10.28.1701. Interpretative drawing of specimen in Figs 5E–G, J. 2A, umbilical view showing the overlapping chamber walls and the preserved apertural slits of the last three chambers; 2B, spiral view; 2C, edge view showing aperture of final chamber, with axis of coiling marked by line A. 2D–F, Paralectotype, 1955.10.28.1700. Interpretative drawing of specimen in Figs 5A–D. 2D, umbilical view showing aperture of final chamber in part masked by agglutinated or secreted material; 2E, spiral view; 2F, edge view of inverted cone-like test with aperture of final chamber in part masked, axis of coiling is indicated by line A. Both × 150.

Both from slide labelled *'Lituola glomerata* Brady'. British North Polar Expedition of 1875–1876. Cape Frazer, lat. 79°45'N, station O, depth 50 fathoms (92 m), ex BMNH slide no. 1955.10.28.1700–1731.

LECTOTYPE. 1955.10.28.1781 (Figs 4A–E). From Brady's syntypic series, obtained from Station P, off Cape Frazer, Arctic Canada, depth 80 fathoms (146 m). Believed to be the specimen figured by Brady (1878, pl. 20, fig. 1b).

DESCRIPTION (LECTOTYPE). Test free; a dextral, tightly coiled trochospire, with 4 chambers in the final whorl, each gradually increasing in size; involute on spiral side. Test a short, broad, inverted cone-like structure, flatly truncated spirally, rounded-convex umbilically, broadly rounded peripherally and somewhat rounded laterally. In edge view, 3 chambers seen on both sides. In spiral/umbilical view, oval-lobate; umbilical side with a small, well-defined subcircular and shallow axial depression. Adult chambers much elongated in axial (edge) view, narrow radially and somewhat elongate tangentially, more inflated towards the spiral, than towards the umbilical side. Intercameral sutures straight but indistinct spirally; straight, distinct, laterally and umbilically. Aperture single, interiomarginal, a narrow elongate slit with rounded extremities, at umbilical end of chamber; symmetrical with respect to its long axis. Border of aperture rests on the first and

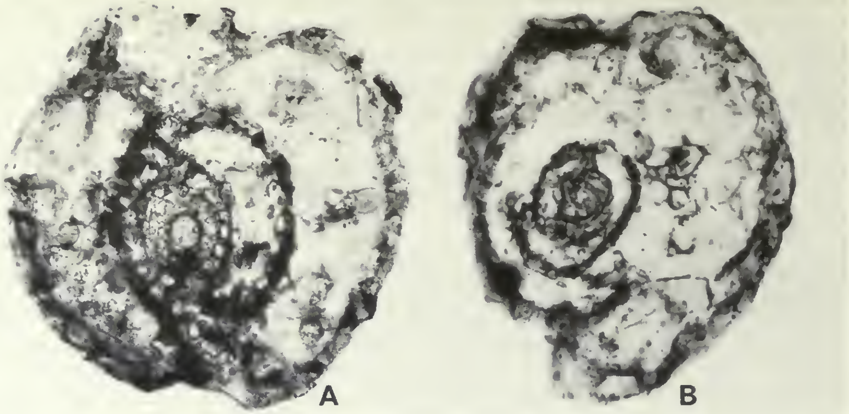


Fig. 3A *Adercotryma glomeratum* (Brady). Paralectotype, 1955.10.28.1782. Section cut parallel to axis of coiling. Note the thin-walled proloculus already slightly elongate in the direction of the coiling axis. × 205.
From Cape Frazer, lat. 79°45′N, station P, depth 80 fathoms (146 m). British North Polar Expedition of 1875–1876, ex BMNH slide no. 1955.10.28.1781–1799, labelled '*Lituola glomerata* Brady'.

Fig. 3B. *Adercotryma wrighti* Brönnimann & Whittaker sp.nov. ZF 4453. Section cut slightly obliquely to axis of coiling. × 250.
From south of Mull, W Scotland, depth 20 fathoms (37 m). S.Y. *Runa* station 2, collected 1913. Heron-Allen & Earland Collection (BMNH), slide labelled '*Haplophragmium glomeratum* (Brady)'.

penultimate chambers of final whorl (*Paratrochammina*-type). Final chamber covers about half of the preceding apertural slit. Wall agglutinated, imperforate, coarser on truncated, spiral side than on rounded-comvex, umbilical side. Colour, prior to coating for SEM photography, yellowish-brown.

DIMENSIONS (LECTOTYPE). Maximum spiral/umbilical diameter 320 μm, minimum diameter 270 μm, height 260 μm. Height of apertural slit c. 12 μm.

PARALECTOTYPES: 3 sinistral specimens (1955.10.28.1700–1702) are figured in Figs 2A–F, 5A–J; another 3 (1955.10.28.1732, 1955.10.28.1783 and 1955.10.28.1703), dissected out to show various aspects of the internal coiling, are figured in Figs 1, 6A–F, whilst a further paralectotype (1955.10.28.1782) has been sectioned and is illustrated in Fig. 3A. These specimens, as with others remaining in Brady's syntypic series, vary considerably in their dimensions, elongation of the chambers in the final whorl, depression of the sutures, depth of the umbilicus and spiral aspect. For further comments, see the figure explanations and Remarks section below. The maximum spiral/umbilical diameter of the figured paralectotypes varies from 230 to 290 μm, the test height, from 250 to 270 μm.

REMARKS. Brady's small and enigmatic species was placed by authors in *Lituola, Haplophragmium, Haplophragmoides* and *Trochammina* prior to the erection of *Adercotryma* by Loeblich & Tappan (1952). The generic changes stem mainly from differing interpretations of the mode of coiling of the curious cone-shaped test.

Although Brady (1878) originally referred to the test as merely '. . . spiral in arrangement', his subsequent comparison (Brady, 1884) of the overall shape with that of a '. . . nautiloid species, such as *Haplophragmium latidorsatum,* drawn out as the umbilici so as to form a test bearing some resemblance to the oval Alveolinae', implied that the coiling was planispiral. He clearly was not sure, however, as he made much in these two papers of the unusual 'unsymmetrical convolutions'.

It was Cushman (1910) who first described the coiling, without reservation, as planispiral, placing Brady's species in his new genus *Haplophragmoides,* an assignment which was generally

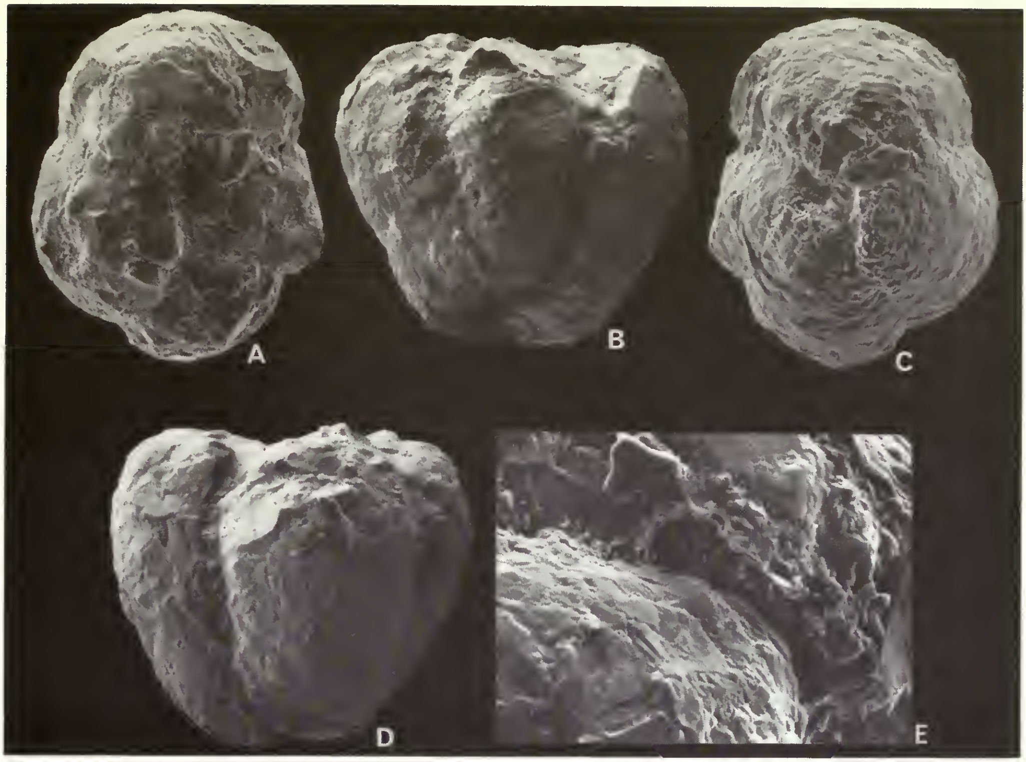


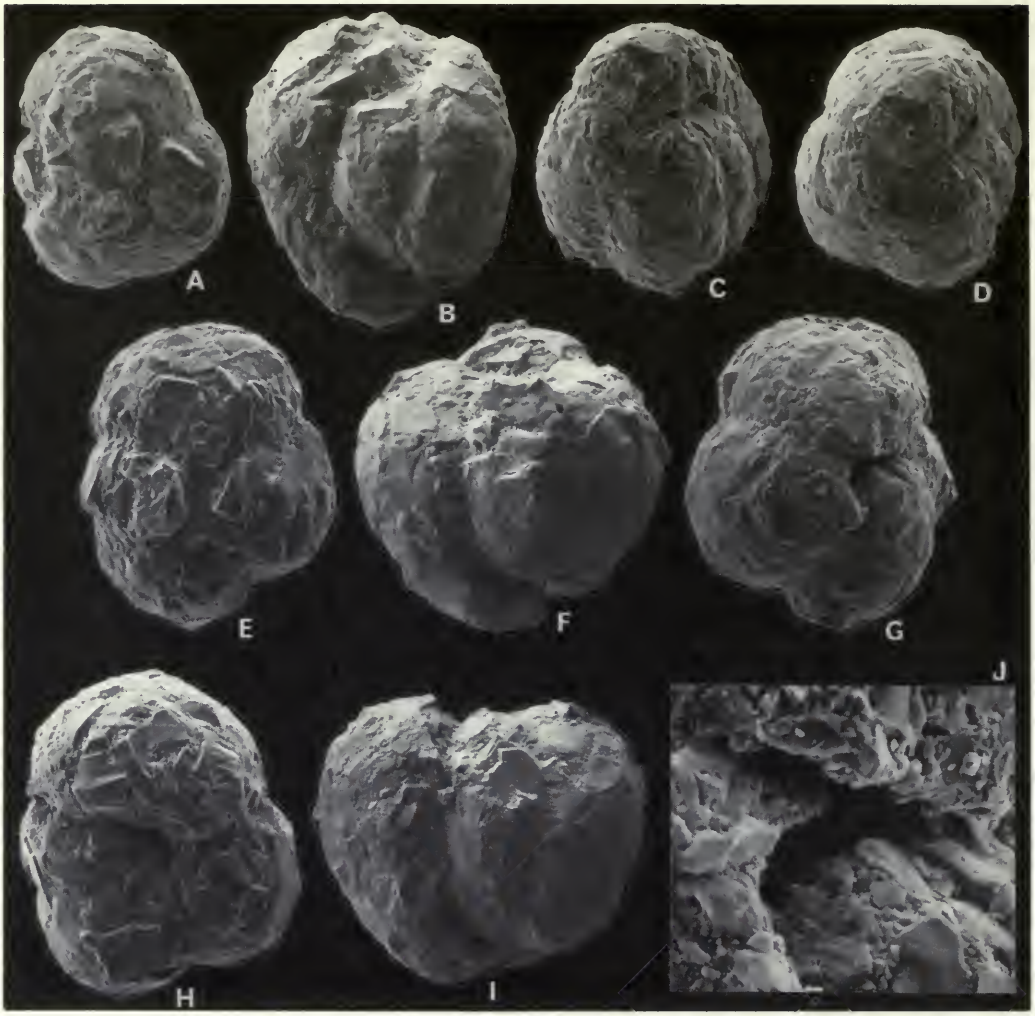
Fig. 4A–E. *Adercotryma glomeratum* (Brady). Lectotype, 1955.10.28.1781. 4A–D, spiral, edge (apertural), umbilical and edge (antapertural) views, × 150. 4E, detail of lateral, open part of aperture, × 525.

From slide labelled '*Lituola glomeratum* Brady'. British North Polar Expedition of 1875–1876. Cape Frazer, lat. 79°45′N, station P, depth 80 fathoms (146 m), ex BMNH slide no. 1955.10.28.1781–1799.

followed for over forty years. The only exception was Wiesner (1931) who placed *glomerata* in *Trochammina,* although he did not make a detailed examination of its morphology and his paper offers no evidence for trochospiral coiling. A year earlier, however, Lacroix (1930) had considered the position of the aperture, ignored completely by Cushman, to be more in keeping with a trochospiral genus. In terms of coiling, Lacroix considered Brady's species transitional between the planispiral *Haplophragmoides* and the trochospiral *Trochammina,* but nevertheless retained it in the former genus.

In 1952, Loeblich & Tappan erected a new lituolid genus *Adercotryma,* with *Lituola glomerata* Brady as type. The name refers to the apertural features, derived from two Greek words *aderco-* unseen, invisible, and *tryma-* meaning a hole or aperture. The gender of the name *Adercotryma* is neuter, and the specific name should be construed as *glomeratum,* not *glomerata* as originally written. Loeblich & Tappan (1952) distinguished their new genus from *Haplophragmoides* on the somewhat asymmetrical, completely involute, rather than slightly evolute test which has its greatest dimension in the axis of coiling, and by its aperture which lies near the umbilicus of one side, rather than in the plane of coiling at the periphery. Of these features, only two are fundamentally different from those of *Haplophragmoides*: the asymmetrical test morphology and the asymmetrical interiomarginal apertural position. In no part of their original paper, nor in 1964, did Loeblich & Tappan discuss the curious asymmetry of what they obviously assumed to be a planispiral test. *Adercotryma* was placed in the Haplophragmoidinae Maync, 1952 (Lituolidae de Blainville, 1825), in which were included both planispiral and streptospiral forms.

Even though the test of *A. glomeratum* is involute, the external and internal morphology clearly

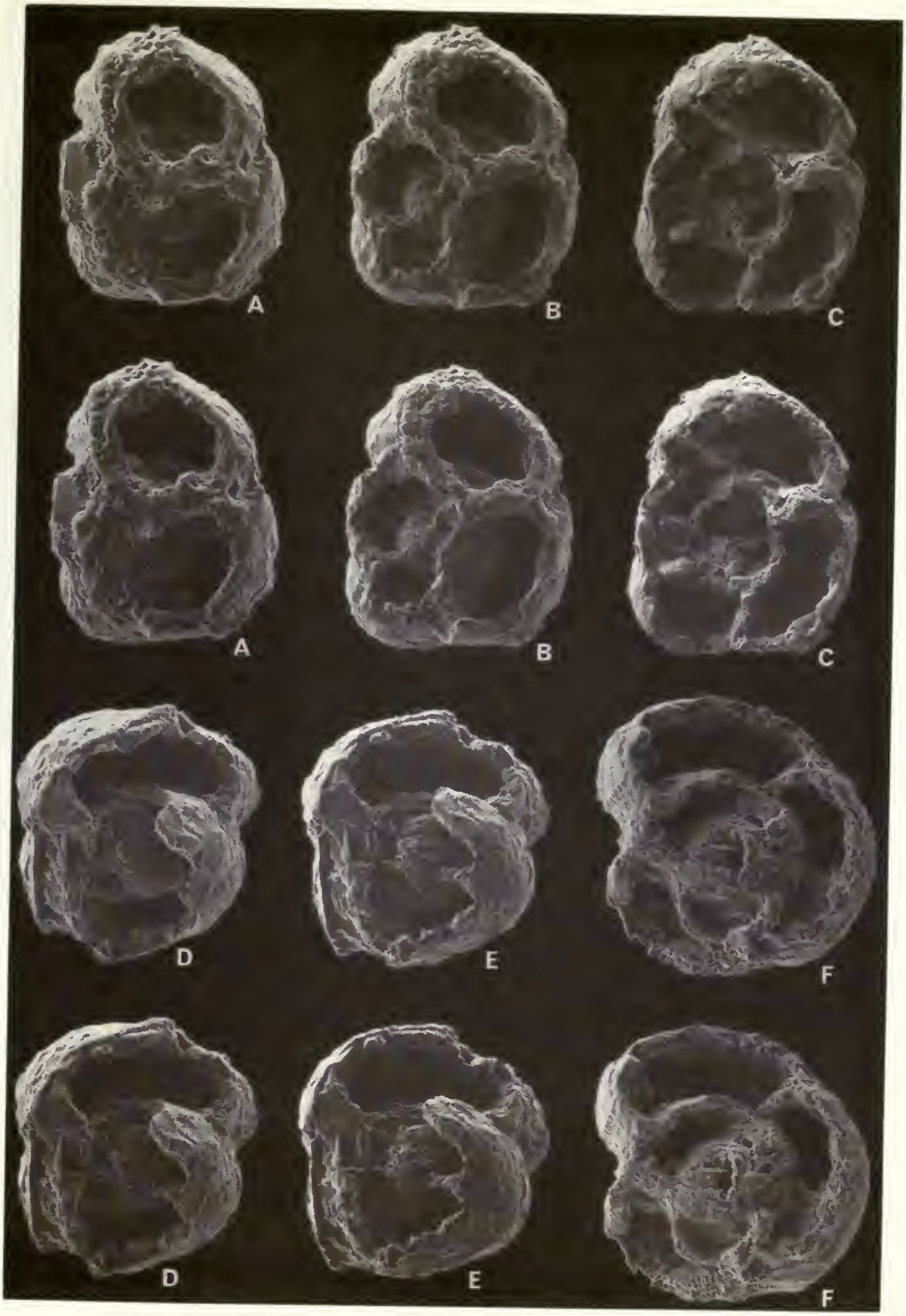


Figs 5A–J. *Adercotryma glomeratum* (Brady). 5A–D, Paralectotype, 1955.10.28.1700. Spiral edge, oblique-umbilical and umbilical views, × 150. 5E–G, J, Paralectotype, 1955.10.28.1701, E–G, spiral, edge and umbilical views, × 150; 5J, detail of interiomarginal apertures of final and penultimate chambers, in umbilical view, × 475. 5H, I, Paralectotype, 1955.10.28.1702. Spiral and edge views, × 150.

All specimens from slide labelled '*Lituola glomerata* Brady'. British North Polar Expedition of 1875–1876. Cape Frazer, lat. 79°45′N, station O, depth 50 fathoms (92 m), ex BMNH slide no. 1955.10.28.1700–1731.

Figs 6A–F. *Adercotryma glomeratum* (Brady). 6A–C, Paralectotype, 1955.10.28.1732. Stereo-pairs of three stages of dissection, perpendicular to axis of coiling; the involute spiral side has been removed. The third stage of dissection (6C) has broken open the earliest whorl and proloculus (see Fig. 1, for interpretative drawing). 6D, E, Paralectotype, 1955.10.28.1783. Stereo-pairs of dissected specimen shown at two different tilts. Dissection is in plane virtually parallel to coiling axis. 6F, Paralectotype, 1955.10.28.1703. Stereo-pair of specimen dissected perpendicular to axis of coiling. All × 150.

Figs 6A–C from Franklin Pierce Bay, lat. 79°28′N, station H, depth 46 fathoms (84 m), ex BMNH slide no. 1955.10.28.1731–1780. Figs 6D, E from Cape Frazer, lat. 79°45′N, station P, depth 80 fathoms (146 m), ex BMNH slide no. 1955.10.28.1781–1799. Fig. 5F, same locality, station O, depth 50 fathoms (92 m), ex BMNH slide no. 1955.10.28.1700–1731. British North Polar Expedition of 1875–1876.



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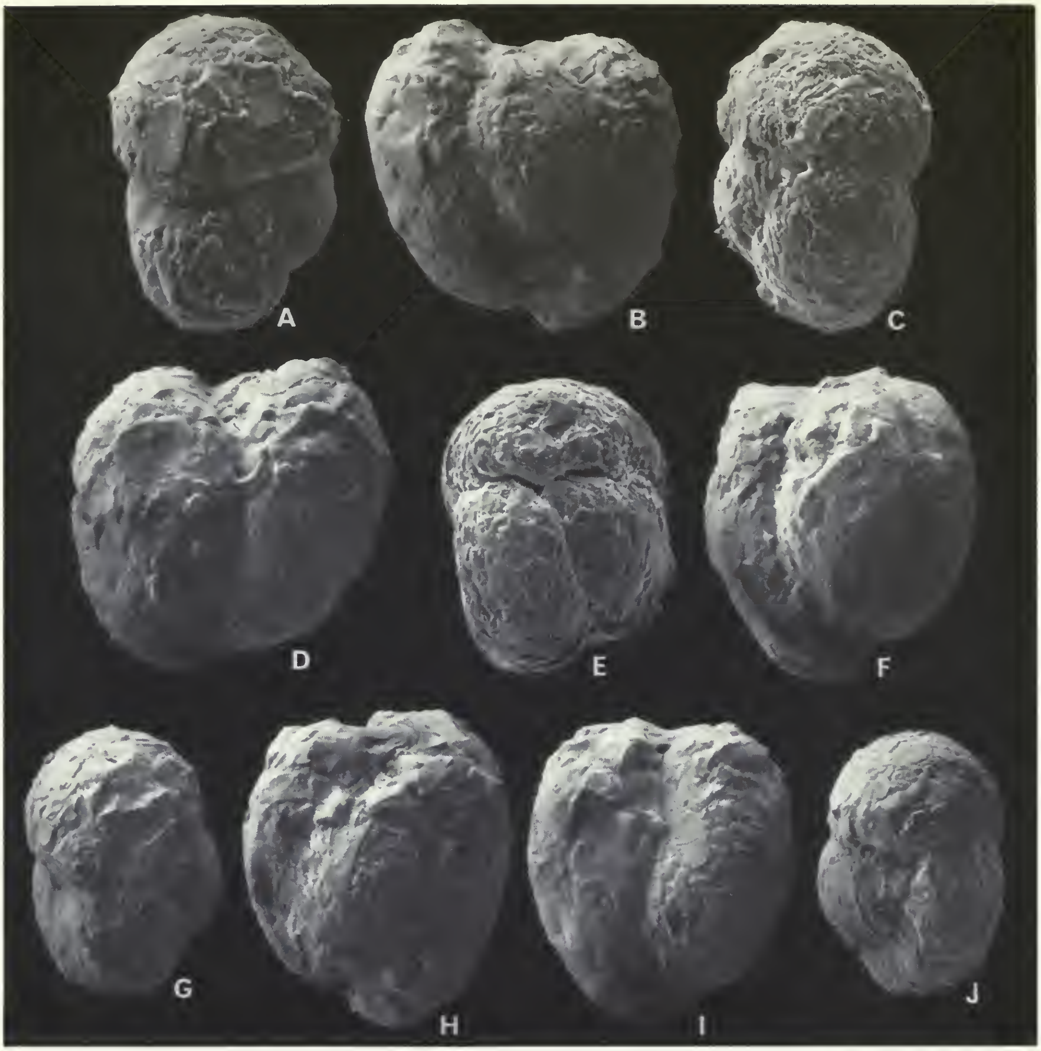

Figs. 7A–J. *Adercotryma wrighti* Brönnimann & Whittaker sp.nov. 7A–D, Holotype, NMI no. 149.1985. Spiral, edge (apertural), umbilical and edge (antapertural) views. 7E, F, Paratype, NMI no. 4.1980. Oblique-umbilical and edge views. 7G–J, Paratype, NMI no. 5.1980. Spiral, edge (apertural), edge (antapertural) and umbilical views. All × 175.

All from off Drogheda, E Ireland, depth 16 fathoms (29 m); ex slide no. 34, labelled 'Dublin: off Drogheda, 16 fms & Lambay Deep, 70 fms (mixed)', J. Wright Collection, 13–1921, National Museum of Ireland.

indicates a trochospiral mode of coiling (Figs 1–6). As well as the asymmetrical aperture, the adult test, when orientated with the axis of coiling in vertical position, shows a truncated, more or less flattened aboral or spiral side, and an obtusely pointed, ovoid-rounded oral or umbilical side. This differentiation is typical of trochospiral tests.

Saidova (1961; 1975) introduced two new subspecies of *A. glomeratum,* namely *A. g. abyssorum* and *A. g. antarctica,* respectively. They are figured together with a typical *A. g. glomeratum* also in Saidova (1975, pl. 96, figs 4–6). The difference in shell morphology said to characterise the two (test size, chamber shape and elongation) falls within the range of variation seen in our paralectotypes (compare our Figs 5B and 5I with Saidova's pl. 96, figs 6 and 5, respectively), whilst the type of agglutinant, also used by Saidova (1961) as a distinguishing feature of *A. g. abyssorum,* is not considered by us to have any taxonomic validity.

A. glomeratum (Brady) differs from *A. wrighti* sp. nov. in having a broadly inverted cone-like test with 4 axially elongate chambers in the final whorl, in the shape of the adult chambers, and in the apertural features. See also pp 27, 28 for further remarks on their differences. In the material studied, *A. glomeratum* always has 4 chambers in the final whorl, even the preceding whorl (Figs 1, 6C) has 4 chambers. This results in 3 chambers being visible on either side of the test when seen in edge view (aperturally and antaperturally).

A. glomeratum is a very wide-ranging species both in terms of latitudinal and depth distribution as noted by Saidova (1975) and Culver & Buzas (1985).

Adercotryma wrighti Brönnimann & Whittaker sp. nov.

Figs 3B, 7A–J

1908 *Haplophragmium glomeratum* (Brady); Millett: 5 (list), pl. 1, fig. 6 (*non Lituola glomerata* Brady, 1878).
1913 *Haplophragmium glomeratum* (Brady); Heron-Allen & Earland: 46, pl. 2, fig. 14.

DIAGNOSIS. A species of *Adercotryma* with only 3 chambers in the final whorl. In spiral/umbilical view, test oval-lobate, maximum diameter often almost twice the minimum diameter. In edge view, 3 chambers seen on apertural side, only 2 on antapertural side. Aperture single, interiomarginal, a bilobed narrow, elongate slit without rounded extremities at umbilical end of chamber.

NAME. In honour of Joseph Wright, in whose collection from Dublin Bay this species was first noticed.

HOLOTYPE. National Museum of Ireland (NMI) no. 149.1985. Illustrated in spiral, edge (apertural), umbilical and edge (antapertural) views in Figs 7A–D. Ex J. Wright Collection, slide 34.

TYPE LOCALITY. Off Drogheda, E Ireland, depth 16 fathoms (30 m).

DESCRIPTION (HOLOTYPE). Test free; a dextral, tightly coiled trochospire, with 3 chambers in the final whorl, gradually increasing in size; involute on spiral side. Test an inverted cone-like structure, truncated spirally, rounded-convex umbilically and broadly rounded peripherally. In edge view, 3 chambers seen on apertural side, 2 on antapertural side. In spiral/umbilical view, oval-lobate, maximum diameter almost twice the minimum diameter; umbilical side with very shallow and small axial depression. Adult chambers elongate in axial (edge) view, less elongate in tangential direction, narrow in radial direction; inflated equally both spirally and umbilically. Intercameral sutures well defined and slightly incurved laterally and umbilically, less well defined and straight spirally. Aperture single, interiomarginal, a bilobed narrow slit without rounded extremities, at umbilical end of chamber, symmetrical with respect to long chamber axis. Border of aperture rests on first and on penultimate chamber of final whorl (*Paratrochammina*-type). Wall agglutinated, imperforate, coarser on spiral side than on umbilical side. Colour of test, prior to coating for SEM photography, orange-brown.

DIMENSIONS (HOLOTYPE). Maximum spiral/umbilical diameter 240 µm, minimum diameter 150 µm, height 220 µm.

PARATYPES. Two paratypes are figured herein. NMI no. 4.1980 (Figs 7E, F) is a sinistral specimen; the aperture is perfectly preserved and shows the bilobed, narrow, elongate slit; the development of a central, triangular lip-like projection of the chamber wall serving to divide the aperture into two virtually identical parts. This specimen has a maximum spiral/umbilical diameter of 220 µm and test height of 240 µm. NMI no. 5.1980, the other illustrated paratype (Figs 7G–J), is dextrally coiled like the holotype. Its maximum spiral/umbilical diameter is 200 µm, the test height 210 µm.

The sectioned specimen (ZF 4453), from the Heron-Allen & Earland Collection, off W Scotland, has a maximum diameter of 220 µm and height of 180 µm; it is figured in Fig. 3B.

REMARKS. *Adercotryma wrighti* sp. nov. is easily distinguished from *A. glomeratum* (Brady) by the overall shape of the test, only 3 chambers in the final whorl, the shape of the adult chambers and the bilobed apertural features formed by the triangular lip-like projection of the chamber wall. *A. glomeratum* always has 4 chambers in the final whorl and a test which in spiral/umbilical aspect has a maximum diameter little greater than the minimum.

Both Millett (1908) and Heron-Allen & Earland (1913) show specimens from W Ireland with only 3 chambers in the final whorl. We have examined their collections and many slides in the Brady and the Norman Collections (BMNH), labelled *Haplophragmium glomeratum* (Brady), from Scotland, Ireland and N England and all exclusively contain *A. wrighti* rather than *A. glomeratum*. Careful study of specimens previously recorded as *A. glomeratum* may extend the present range of *A. wrighti* beyond the British Isles.

Acknowledgements

The Director of the National Museum of Ireland is thanked for his permission to borrow and photograph specimens from the Wright Collection; Mr J. M. C. Holmes facilitated the loan. We are pleased to acknowledge the technical skill of Mr R. L. Hodgkinson, British Museum (Natural History), in preparing the dissections and thin sections of the *Adercotryma* spp.; Mrs L. M. McCormick and Mr P. V. York took the SEM and optical photographs, respectively, whilst Drs C. G. Adams and M. K. Howarth, also of the same institution, kindly read the manuscript and suggested many improvements. The research of P. Brönnimann is in part funded by the Fonds National Suisse.

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Hermit crabs associated with the bryozoan *Hipporidra* in British waters

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The cheilostome bryozoan *Hippoporidra lusitania* is not associated exclusively with the hermit crab *Pagurus cuanensis* as some previous reports have implied. It has been found with two other species of pagurid, *Anapagurus chiroacanthus* and *Cestopagurus timidus*; its occurrence with *P. cuanensis* requires confirmation.

Species of the cheilostome bryozoan genus *Hippoporidra* preferentially or exclusively encrust gastropod shells inhabited by hermit crabs (Crustacea: Anomura: Paguroidea). Helicospiral growth of an established bryozoan colony may extend the crab's domicile well beyond the aperture of the original gastropod shell (Taylor & Cook, 1981). The type-species of the genus, *Hippoporidra edax* (Busk), was first described as a fossil from the Coralline Crag (Pliocene) of eastern England, but the name has subsequently been used for living specimens from both sides of the North Atlantic. However, material from Recent British seas that had formerly been referred to *H. edax* was distinguished as a new species, *H. lusitania*, by Taylor & Cook (1981).

No details were given by Taylor & Cook (1981) of the hermit crabs with which *H. lusitania* occurs. A few earlier records of Recent *Hippoporidra edax* from Britain, which may be assumed to refer to *H. lusitania*, mentioned *Pagurus cuanensis* Bell as the associated pagurid. Thus, Moore (1937) reported a single colony of the bryozoan with *P. cuanensis* collected off the Isle of Man. This record was repeated by Bruce *et al.* (1963) and quoted by Cook (1964). Eggleston (1972) reported that in Manx waters *Hippoporidra* was in fact restricted to *P. cuanensis*, and this apparent example of extreme stenotopy in a bryozoan was quoted by Ryland (1976). Hayward & Ryland (1979) gave *P. cuanensis* as the preferred species of British *Hippoporidra*, and did not name any other pagurid with which the bryozoan was found.

The Bryozoa collection of the Zoology Department of the British Museum (Natural History) contains 21 colonies of *H. lusitania*, including the type series from Guernsey and part of the Manx material studied by Eggleston. The associated hermit crab is present in only four examples, as detailed in Table 1.

It is clear from this that *H. lusitania* is not restricted to *Pagurus cuanensis*, even off the Isle of Man. Indeed, its occurrence with *P. cuanensis* at all requires confirmation. *P. cuanensis* reaches a considerably larger size than either *Anapagurus chiroacanthus* (Lilljeborg) or *Cestopagurus timidus*

Table 1

Specimen			H	W	Hermit crab
Isle of Man	D. Eggleston	1963.12.30.1	11·0	11·5	*Anapagurus chiroacanthus*
Guernsey	A. M. Norman	1911.10.1.1143H (Paratype)	12·0	10·0	*Anapagurus chiroacanthus*
Guernsey	A. M. Norman	1911.10.1.1143I (Paratype)	8·5	8·5	*Anapagurus* sp. (fragment)
Scilly Isles	M. H. Thurston	1965.8.18.26	7·5	4·5	*Cestopagurus timidus*

H = approximate height of gastropod/bryozoan measured along axis, in mm.
W = approximate 'body whorl' diameter of gastropod/bryozoan, in mm.

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(Roux), the carapace lengths given by Bouvier (1940) being 8–12 mm, 4–6 mm and 4–5 mm respectively. All *H. lusitania* colonies available for study at the BM(NH) are relatively small; the largest (Plymouth, T. Hincks, 1899.5.1.1517) has a height of *c.* 17 mm and a 'body whorl' diameter of *c.* 14 mm. It therefore seems probable from the limited material available that *Hippoporidra lusitania* may be most commonly associated with relatively small hermit crabs.

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The first zoea of three *Pachygrapsus* species and of *Cataleptodius floridanus* (Gibbes) from Bermuda and Mediterranean (Crustacea: Decapoda: Brachyura)

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Introduction

Affinities of larvae belonging to the family Grapsidae have been reviewed by Aikawa (1929), Wear (1970), Rice (1980) and Wilson (1980). Within the four subfamilies composing this family 'the larval development of less than 15% of all the species has been described' (Wilson, 1980: 756). Many descriptions are insufficient for meaningful comparative studies and, because of the apparent difficulty of rearing these small zoeae, a large percentage of studies describe only the first stage.

Wilson (1980) has provided a useful and comprehensive table of seven comparative features of the first stage zoeae of 47 grapsid species. To this list may be added the following accounts which contain more or less adequate details for comparative purposes. Plagusiinae: ?*Plagusia depressa,* Rice & Williamson, 1977. Varuninae: *Eriocheir japonica, Gaetice depressus, Hemigrapsus longitarsus, H. penicellatus, H. sanguiensis,* Terada, 1981. Grapsinae: *Metopograpsus latifrons,* Kakati, 1982; *M. messor,* Rajabai, 1962. Sesarminae: *Aratus pisonii,* Hartnoll, 1965; *Chasmagnathus convexus,* Saba, 1974; *C. laevis, Helograpsus haswellianus,* Green & Anderson, 1973; *Metasesarma rousseauxi,* Rajabai, 1962; *Sesarma erythrodactyla,* Green & Anderson, 1973; *S. perracae,* Soh Chen Lam, 1969; *S. tetragonum,* Rajabai, 1962.

Within the genus *Pachygrapsus* larval stages are known for only three of the fifteen or so accepted species (viz. *P. marmoratus, P. transversus, P. crassipes*). Of these, the complete development has been described for *P. marmoratus* (Fabricius) and *P. crassipes* Randall. Larval descriptions of *P. marmoratus* are based, except for the first stage, upon plankton collected material (see Cano, 1892; Hyman, 1924; Bourdillon-Casanova, 1960), but some of Cano's figures, also reproduced by Hyman, may not even be of a *Pachygrapsus* (see p. 000). Laboratory hatched first stage zoea of *P. transversus* was described superficially by Lebour (1944) and Rossignol (1957) identified a plankton caught megalopa to this species. Villalobos (1971) described the first zoeal stage of *P. crassipes.* This species was laboratory reared to fifth zoeal stage by Schlotterbeck (1976) and a plankton caught megalopa was tentatively assigned to *P. crassipes* by Rathbun (1923).

During 1973 first stage zoeae of *Pachygrapsus marmoratus* were obtained from a laboratory held crab collected by R. B. Manning off the coast of Tunisia and in 1983 the first stage zoeae of *P. gracilis* and of *P. transversus* were hatched from crabs held by the author in the Biological Station, Bermuda. Although the larvae of these species were not reared beyond the first zoeal stage it would seem desirable to give an account of this material to supplement meagre larval information at present available on this genus and also to compare (see Table) the first stages of these four *Pachygrapsus* species. Opportunity is also taken to describe the first stage zoea of the xanthid *Cataleptodius floridanus* (also hatched at Bermuda), the larvae of which were studied by Kurata (1970) but whose account was never published (see Martin 1984: 233, footnote).

Materials and methods

The first zoea of *P. marmoratus* was hatched from a crab collected in the canal leading from

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Table 1. Comparative features of *Pachygrapsus* first zoeal stage

FEATURE	*P. gracilis* (present material)	*P. tranversus* (present material)	*P. crassipes* (Schlotterbeck 1976)[1]	*P. marmoratus* (present material)
Dorsal spine/C.L:	0·60–0·70 mm	0·60–0·70 mm[2]	0·90 mm	0·75 mm[3]
Carapace, posterio-lateral margins	denticles conspicuous	denticles inconspicuous	denticles conspicuous	denticles very inconspicuous[4]
Antennule, aesthetascs/setae numbers	4	4[5]	3	4
Antenna, spinous process investment	denticles few and obtuse on distal part	denticles numerous long and subacute on distal part	two small acute denticles only on distal part	denticles small[6] acute and numerous on distal part
Maxilla, coxal endite, setae	9 (4+5)	9 (4+5)	?8 (4+4)[7]	9 (4+5)
Abdomen, fourth segment	laterally expanded, with obtuse dorso-lateral processes	laterally expanded, with obtuse[8] dorso-lateral processes	slightly laterally expanded, with minute dorso-lateral processes	not laterally expanded dorso-lateral processes absent[9]
Telson, lateral spines on furcae	both very minute	minute, one larger than[10] the other	absent	absent[11]

[1] Schlotterbeck tabulates several additional features by which his account differs from the one given by Villalobos (1971); [2] Lebour (1944) gives 0·9 mm; [3] Bourdillon-Casanova (1960) gives 1·10 mm and [4] shows these denticles as conspicuous; [5] Lebour shows 3 setae; [6] Bourdillon-Casanova shows these as conspicuous; [7] Villalobos states 7 setae; [8] Lebour shows these as large, curved and acute; [9] the conspicuous processes shown on this segment by Bourdillon-Casanova are the large denticles on the posterio-lateral margins (see Fig. 3h inset); [10] Lebour shows these equally developed; [11] Bourdillon-Casanova shows these as very conspicuous although 'très fines', they are absent in all specimens examined.

southern Punic Port, Salammbo, Tunisia, 18.7.1973. Ovigerous *Pachygrapsus gracilis* and *Cataleptodius floridanus* were collected at various localities from the intertidal mud flats at Ferry Reach and *P. transversus* from beneath stones at Whalebone Bay, Bermuda, all in September/October 1983. The eggs hatched within 2–3 days of the crab's confinement in aerated aquaria water held at 20–24°C and the larvae were fed newly hatched *Artemia* nauplii. Live zoeae were subsequently transported to a rearing laboratory at the British Museum (Natural History) in London but none survived to the second stage.

Measurements given are: T.T. = distance between tips of dorsal and rostral spines; C.L. = carapace length from between the eyes to the posterio-lateral margin. The material has been incorporated in the Collections of the British Museum (Natural History), accession number: 1985: 463–468.

Descriptions

Family **GRAPSIDAE** MacLeay, 1838
Subfamily **GRAPSINAE** MacLeay, 1838

Pachygrapsus gracilis (de Saussure, 1858)

Dimensions: T.T. 0·60–0·70 mm. C.L. 0·35–0·38 mm.
Carapace (Fig. 1a): dorsal spine short and straight, stout proximally, slightly more than one third carapace length; rostral spine of moderate length and stout; dorso-median elevation prominent; at least four pairs of anterio-median setules and a pair of posterio-median setules present; posterio-lateral margins of carapace narrowly rounded with 3–4 obtuse denticles and lateral microscopic setules (inset to fig.).
Eyes: partly fused to carapace.
Antennule (Fig. 1b): unsegmented with four aesthetascs/setae.
Antenna (Fig. 1c): spinous process as long as rostral spine and with many subacute denticles; exopod very small, about one ninth of spinous process length.
Maxillule (Fig. 1d): endopod 2-segmented, proximal segment with one seta, distal with one subterminal and four terminal setae; basial endite with five spines, coxal with six spines/setae.
Maxilla (Fig. 1e): endopod stepped distally, outer lobe broader than inner each with two long setae; basial endite incipiently bilobed distally, each with four setae; coxal endite bilobed distally, outer lobe with four and inner with five setae respectively, seta on apex of outer lobe very short almost a spine; scaphognathite with four plumose setae and a stout posterior process.
First maxilliped (Fig. 1f): basis with eight setae arranged in pairs; endopod five-segmented with 1, 2, 1, 2, 4 + 1 setae; exopod incipiently two-segmented and with four terminal plumose setae.
Second maxilliped (Fig. 1g): basis with four setae; endopod three-segmented with 0, 1, 4 + 1 setae; exopod incipiently two-segmented with four terminal plumose setae.
Third maxilliped and *pereiopods*: not developed.
Abdomen (Fig. 1h): composed of five segments and a telson, somewhat dorso-ventrally compressed, surfaces with microscopic spinules; second and third segments with a pair of broad dorso-lateral processes; fourth segment laterally expanded and with a pair of obtuse lateral processes placed at a lower level than the ones on preceding segments; first segment, posterio-lateral margins truncate, those of other segments obtuse and of third to fifth with a very minute denticle; second to fifth segments each with a pair of setules near posterio-dorsal margin. Telson somewhat narrowed, furcae not noticeably directed outwards, each with numerous microscopic spinules and two very small lateral spinules; posterior margin with six equal plumose setae.

Pachygrapsus transversus (Gibbes, 1850)

Pachygrapsus transversus: Lebour, 1944: 115, fig. 5 (zoea I); Rossignol, 1957: 89, fig. 5 (megal.).

Dimensions: T.T. 0·60–0·70 mm. C.L. 0·30–0·35 mm. Differs from *P. gracilis* in the following features.
Carapace (Fig. 2a): dorsal spine longer and proximally slightly stouter, more than one third of carapace length; rostral spine noticeably stouter proximally; posterio-lateral margin of carapace with very inconspicuous denticles and with microscopic setules; only two pairs of anterio-median setules apparent.
Antenna (Fig. 2c): spinous process with numerous subacute denticles developed distally as stout spine-like processes; exopod about one seventh of spinous process length.
Maxillule (Fig. 2d): spines/setae slightly stouter.
Maxilla (Fig. 2e): basial endite noticeably bilobed distally.

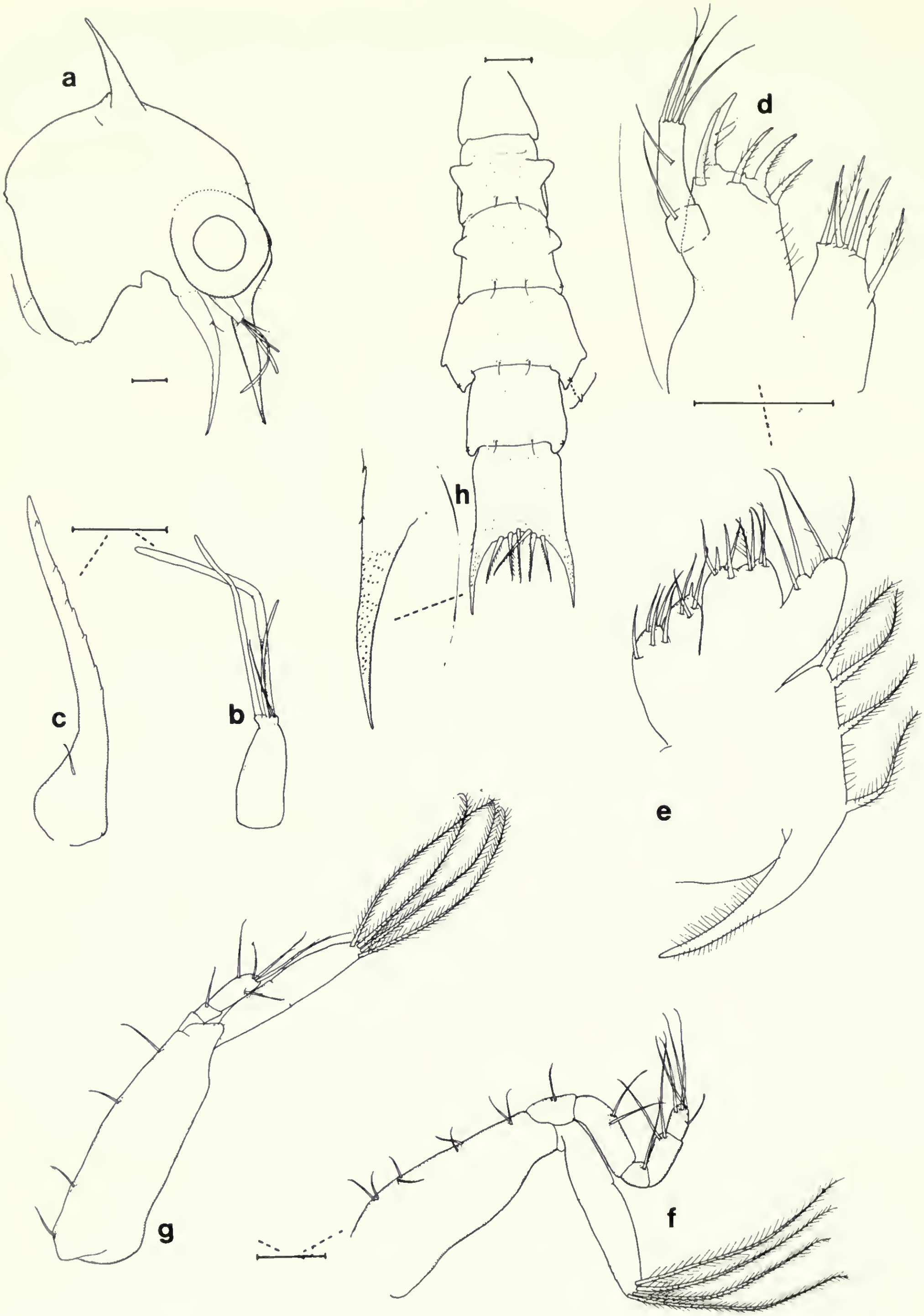

Fig. 1. *Pachygrapsus gracilis* (de Saussure). First zoea. a, carapace, right lateral aspect; b, antennule; c, antenna; d, maxillule; e, maxilla; f, first maxilliped; g, second maxilliped; h, abdomen and telson, dorsal aspect. Scale = 0·05 mm.

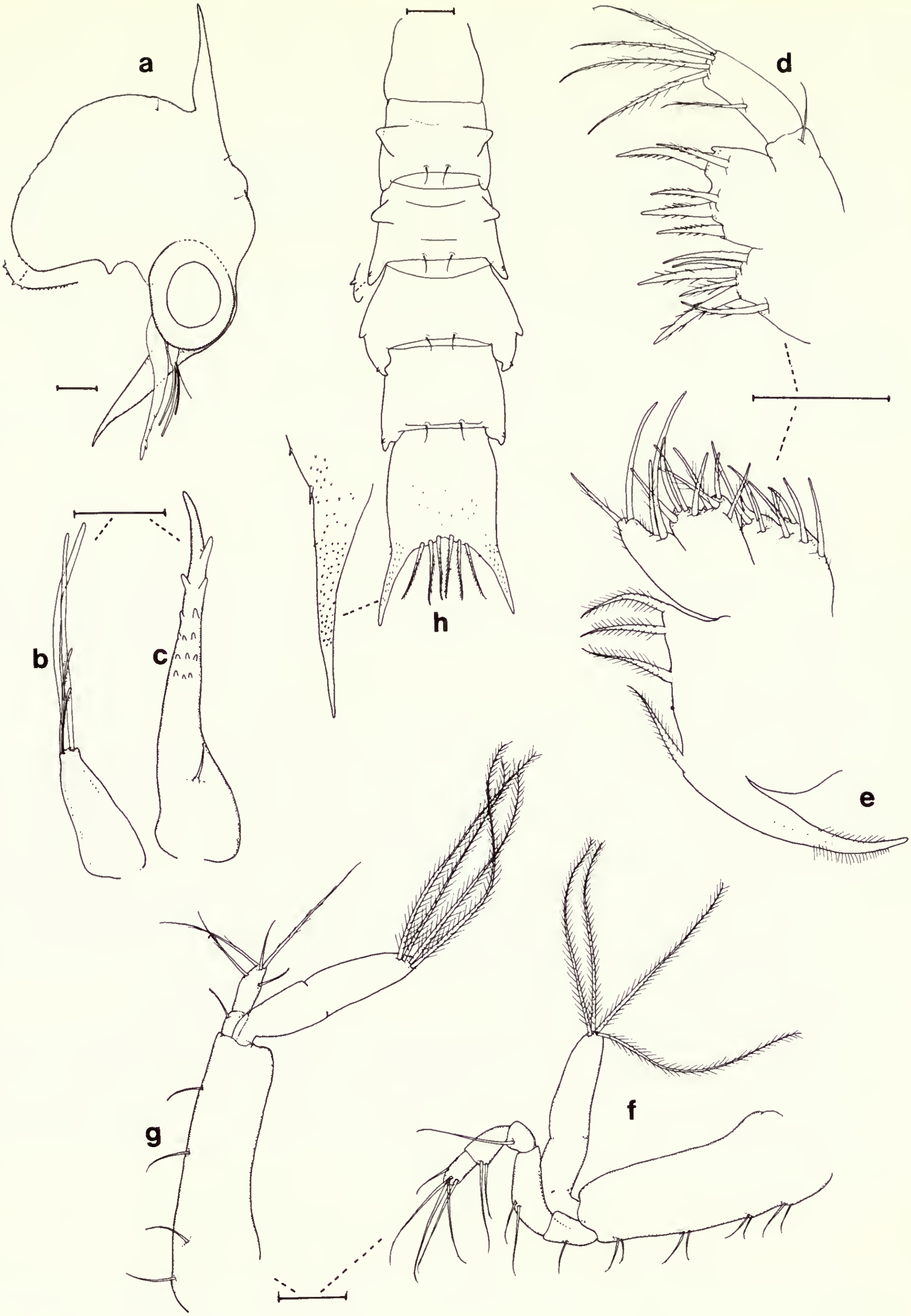

Fig. 2. *Pachygrapsus transversus* (Gibbes). First zoea. a, carapace, right lateral aspect; b, antennule; c, antenna; d, maxillule; e, maxilla; f, first maxilliped; g, second maxilliped; h, abdomen and telson, dorsal aspect. Scale = 0·05 mm.

Abdomen (Fig. 2h): slightly larger, posterio-lateral margins of fourth segment subacute and of the other segments (except first) more produced, denticles larger. Telson slightly broader, the more posterior of the two lateral spinules larger; furcae slightly shorter and stouter.

Pachygrapsus marmoratus (Fabricius, 1787)

Pachygrapsus marmoratus: Cano, 1892: 8.Tav.III, figs 1B (?zoea III), ?1C, 1E, 1F, ?2c, 2e–f, ?3c, 4e–f, 5e–f, 6e–f, 7e–f, 8e–f (labelled as 6 in fig.), 12e, 13e, 14e, 15e (?zoea IV, megal.); Williamson, 1915: 518, figs 403–405, 407–8 (figs after Cano); Hyman, 1924: 2, Pl. 3, figs 22, ?23, 25, 26, ?33, 36a–b, 41, 42, 44, 45, 48, 49, 50, 52, 53, 54, 56 (figs after Cano): Bourdillon-Casanova, 1960: 188, fig. 61 (zoea I); Paula, 1985: 142, fig. 3 (zoea I).

Dimensions: T.T. 0·75 mm. C.L. 0·35 mm.
Differs from *P. gracilis* and *P. transversus* as follows.
Carapace (Fig. 3a): dorsal spine longer, exceeding half carapace length; posterio-lateral margin of carapace without setules, denticles very minute; anterio-median setules not apparent.
Antenna (Fig. 3c): denticles on spinous process small and numerous throughout length of process.
Maxillule (Fig. 3d): setules on spines/setae very long.
Abdomen (Fig. 3h): fourth segment not laterally expanded and without a pair of obtuse lateral processes; posterio-lateral margins of third to fifth segments each with a conspicuous denticle. Telson lateral spinules on furcae absent.

Family **XANTHIDAE** MacLeay, 1838

Cataleptodius floridanus (Gibbes, 1850)

Dimensions: T.T. 1·1 mm. C.L. 0·43 mm.
Carapace (Fig. 4a): dorsal spine long, distally curved, proximally stout; rostral spine almost as long as dorsal spine and with 1 or 2 small spinules; lateral spines small; dorso-median elevation hardly developed; no anterio-median setules apparent, a small pair of posterio-median setules present; posterio-lateral margin of carapace with one or two small setules.
Eyes: partly fused to carapace.
Antennule (Fig. 4b): unsegmented and with four aesthetascs/setae.
Antenna (Fig. 4c): spinous process as long as rostral spine, distally with many long acute spines; exopod small, between one sixth and one seventh of spinous process length and with two small distal setules.
Maxillule (Fig. 4d): endopod two-segmented, proximal segment with one distal seta, distal segment with five setae (two subdistal and three distal); basial endite with five spines/setae; coxal endite with seven setae.
Maxilla (Fig. 4e): endopod two-lobed, outer slightly stepped, broader than inner and with 2+2 setae, inner lobe with three setae; basial endite two-lobed, outer prominent and with four setae, inner with five setae; coxal endite two-lobed each with four setae; scaphognathite with four plumose setae and a stout posterior process.
First maxilliped (Fig. 4f): basis with ten setae arranged 2, 2, 3, 3, respectively; endopod five-segmented, with 3, 2, 1, 2, 4+1 setae respectively; exopod incipiently two-segmented with four terminal plumose setae.
Second maxilliped (Fig. 4g): basis with four setae; endopod three-segmented, with 1, 1, 4+1 setae respectively; exopod incipiently two segmented, with four terminal plumose setae.
Third maxilliped and *pereiopods*: not developed.
Abdomen (Fig. 4h): composed of five segments and a telson; second segment with a pair of subacute laterally directed dorso-lateral processes, third segment with a pair of small acute posteriorly directed dorso-lateral processes; posterio-lateral margins of second segment acute, those of third to fifth segments extended into acute processes; posterio-dorsal surface of second to fifth segments each with a small pair of setules near margin; posterior margins of segments four and five with minute denticles. Telson furcae diverging slightly, each with one long prominent dorsal spine and one long and one smaller lateral spine, furcae with minute denticles; posteror margin of telson with six long setae.

Remarks

As mentioned earlier, some of the stages described and figured by Cano (1892) as *Pachygrapsus marmoratus* may not belong to this species. His figure depicting a first stage zoea (Tav.III, Fig. 1A) does not show a dorso-lateral process on the third segment of the abdomen characteristic of *Pachygrapsus* zoeae and obvious in the present laboratory reared material. Cano's figure IB clearly shows this lateral process and although this larva is depicted with four maxillipedal exopod setae it

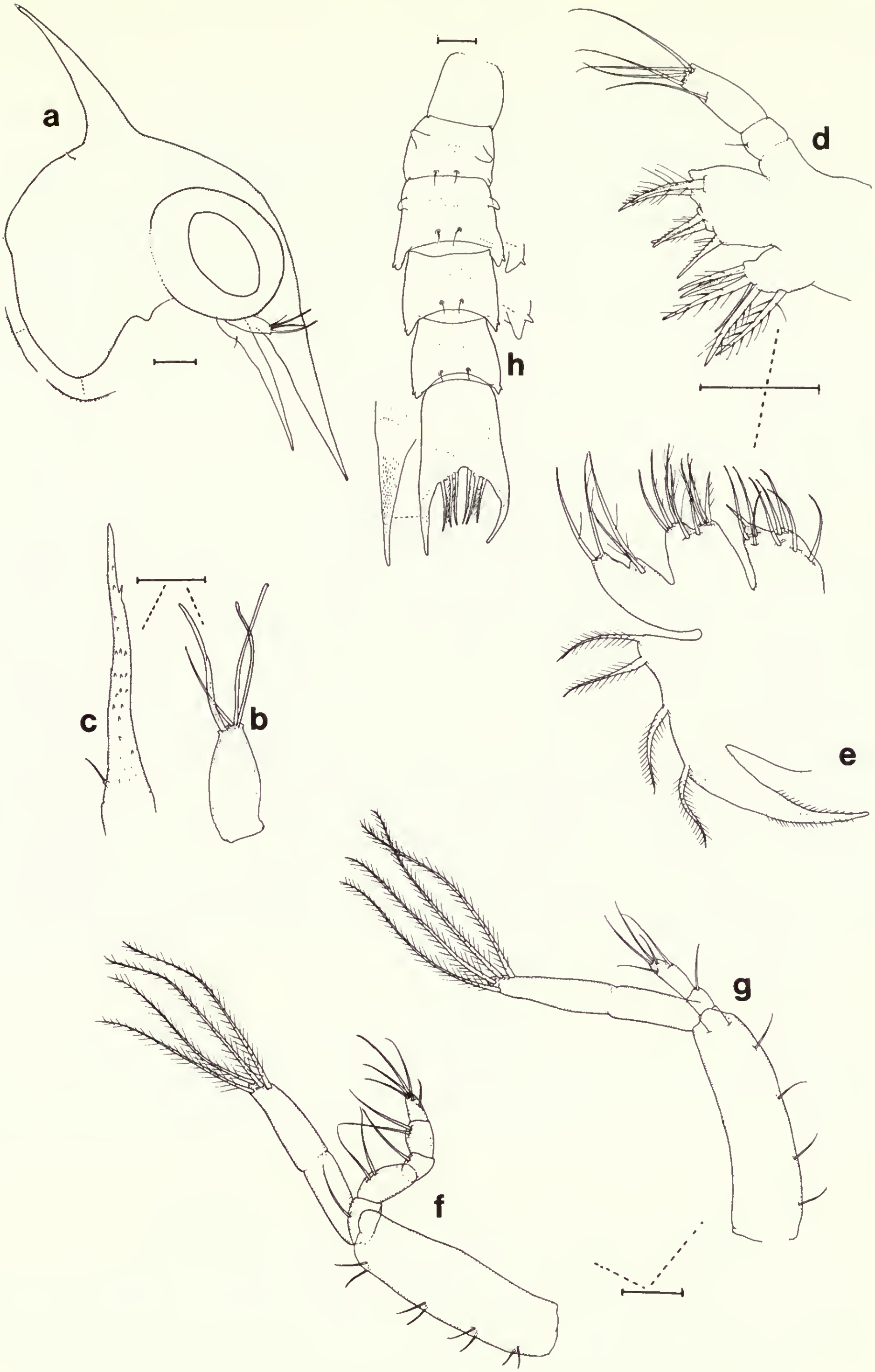

Fig. 3. *Pachygrapsus marmoratus* (Fabricius). First zoea. a, carapace, right lateral aspect; b, antennule; c, antenna; d, maxillule; e, maxilla; f, first maxilliped; g, second maxilliped; h, abdomen and telson, dorsal aspect. Scale = 0·05 mm.

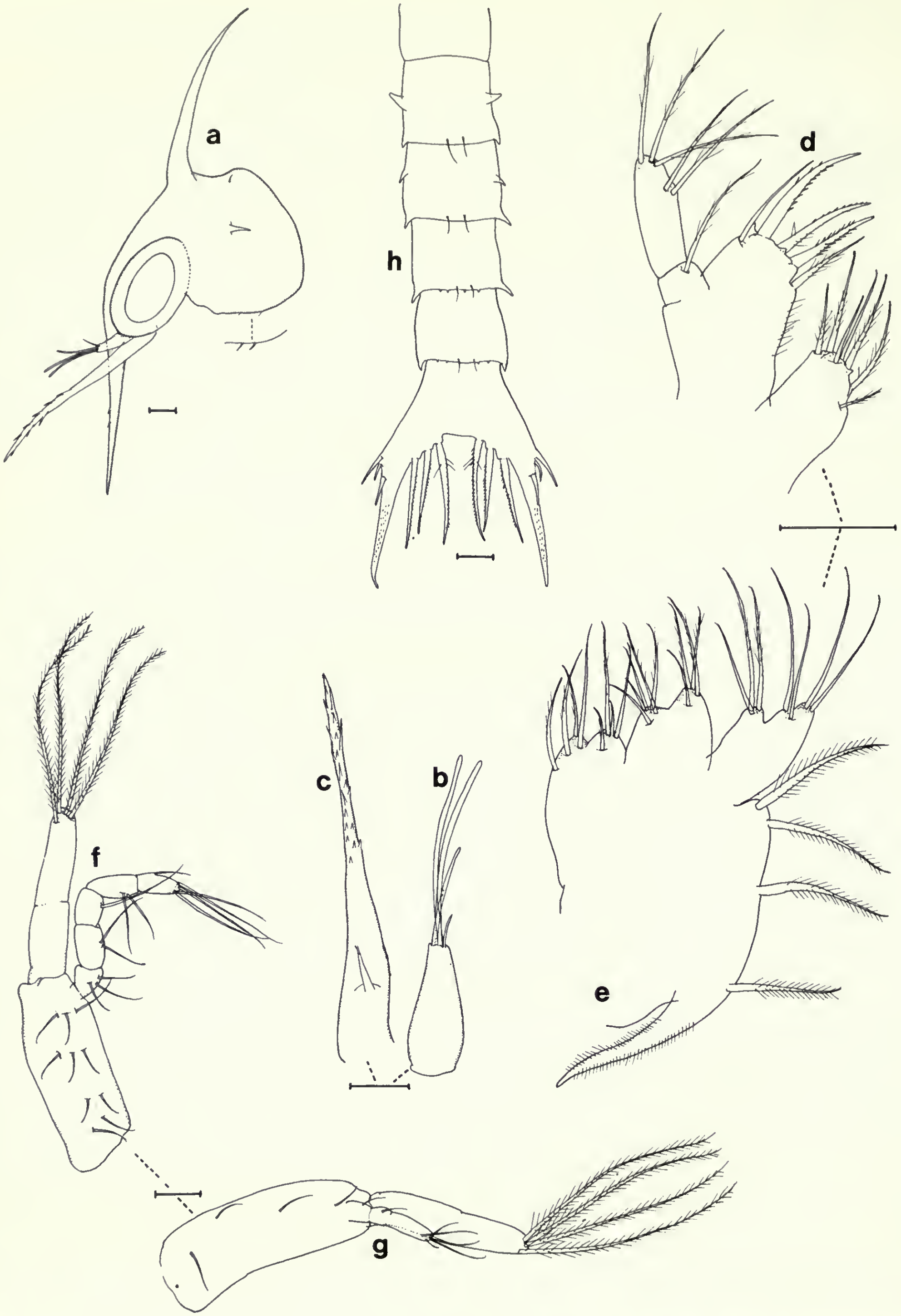

Fig. 4. *Cataleptodius floridanus* (Gibbes). First zoea. a, carapace, left lateral aspect; b, antennule; c, antenna; d, maxillule; e, maxilla; f, first maxilliped; g, second maxilliped; h, abdomen and telson dorsal aspect. Scale = 0·05 mm.

is probably of a later stage because he figures incipient pereiopods beneath the carapace. Hyman (1924) has suggested that this is a stage three zoea and was also convinced that Cano had overlooked a fourth stage and that the third stage described by Cano (purporting to be the last) represented the fifth and terminal zoeal stage of this species. Costlow & Bookhout (1962) however, maintained that . . . 'While some of Cano's (1891) figures may bear some slight inaccuracies, it is quite possible that the sequence and number of larval stages which he figures is correct. . .' These views were expressed in the context of their study of the larval development of *Sesarma reticulatum* in which there are only three zoeal stages and it is probable that *P. marmoratus* passes through five stages similar to *P. crassipes.* Cano (1892) also assigned two megalopal forms to *P. marmoratus.* The one illustrated in his fig. ID and bearing an acute rostral projection appears to be of an oxyrhynch as it lacks dactylar subterminal setae on the fifth pereiopods characteristic of brachyrhynch megalopas. Bourdillon-Casanova (1960) described the first stage zoea of *P. marmoratus* from laboratory hatched material and illustrated (Fig. 61) prominent denticles on the carapace posterio-lateral margin as well as two conspicuous lateral setae (also shown by Paula, 1985, Fig. 3,i) on each furca of the telson. These two features could not be detected in specimens examined during the present study. Lebour's (1944) figure of the first zoea of *P. transversus,* also obtained from Bermudan laboratory hatched crabs, differs from the present specimens in apparently having two distal setae on the antennal spinous process, a pair of conspicuous curved, acute dorso-lateral processes on the fourth abdominal segment and two equally developed lateral spinules on the telson furca. Her zoeae were also larger than the present ones.

Mid-dorsal carapace setules have never been mentioned previously as occurring in *Pachygrapsus* zoeae, and Gore & Scotto (1982: 518) suggested they may be absent in grapsinid zoeae. However in the present study these setules were found in first stage zoeae of *P. gracilis* and *P. transversus* but were not apparent in *P. marmoratus.* They are somewhat difficult to resolve satisfactorily, even with the aid of interference contrast, but appear to be less numerous on the anterio-median region of *P. transversus* than of *P. gracilis.* In many brachyuran larvae these setules do not appear until later stages.

Martin (1984: 232–233) has provided an excellent key to the known xanthid zoeae of the Western Atlantic and Gulf of Mexico. The present study confirms his assessment of the larvae of this species as belonging to his group I of the xanthidae and they can be assigned to *C. floridanus* on the following combined features: (1) lateral processes of third to fifth abdominal segments not extending posteriorly beyond half length of following segment, (2) more than twenty spinules on spinous process of antenna, (3) abdominal dorso-lateral processes confined to second and third segments, (4) telson with three spines on each furca, (5) lateral carapace spines present, (6) basial segment of first maxilliped endopod with three setae, (7) antennal exopod very reduced.

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A classification of the phylum Sipuncula

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Synopsis

A classification of the phylum Sipuncula is adopted following the analysis of Cutler & Gibbs (1985) and comprises two classes, four orders and six families. This replaces the earlier classification of Stephen & Edmonds (1972) which was based on four families only. The diagnostic characters are reviewed. Seventeen genera are redefined, one new subgenus is described and twelve other subgenera are recognised.

Introduction

The classification of the phylum Sipuncula has had a confused history. Early attempts to define higher taxa by grouping genera were, to a large extent, thwarted by incomplete, imprecise or erroneous descriptions of many species. Stephen & Edmonds (1972) classified the phylum into four families in providing the first compilation of species described prior to about 1970. However, this monograph is essentially literature-based and consequently many errors are repeated; nevertheless, it provides a useful base-line to the present revision.

The need for greater precision in defining genera has led the authors to re-examine most of the available type specimens. The definitions of genera presented below incorporate both novel observations and corrections to earlier descriptions. Where possible, nine basic characters have been checked for each species before assigning it to a genus. These characters are summarised for each genus in Table 1. A phylogenetic interpretation of the classification used here will be found in Cutler & Gibbs (1985).

Diagnostic features of higher taxa

In reviewing the diagnostic characters of the phylum, particular attention has been paid to the structure of the oral disk since the arrangement of the tentacles provides a useful basis for dividing the phylum into two classes – Sipunculidea and Phascolosomatidea. Certain descriptions of tentacle arrangements are misleading or in error (see for example Stephen & Edmonds (1972) p. 16 and Table 3). No doubt these errors result from the fact that some species are not amenable to fixation in the extended state; species with long introverts are notoriously difficult to preserve with their introvert fully extended. Although dissection of the introvert is possible the details of the tentacular arrangement on a withdrawn disk are often difficult to interpret and have yet to be satisfactorily determined in some small-sized species (e.g. *Apionsoma trichocephala* Sluiter). The following summarises the distinctions of the two classes.

The sipunculan tentacular crown exhibits many diverse forms but, basically, two tentacular patterns can be recognised. In one, that of the proposed class Sipunculidea, the tentacles are arranged peripherally on the oral disk so as to encircle the centrally-placed mouth; dorsally this circle is inflected to form an arc enclosing the nuchal organ, a feature well developed in *Thysanocardia* spp for example (see Gibbs, Cutler & Cutler, 1983, Fig. 2). In the other, that of the proposed class Phascolosomatidea, the tentacles are restricted to a dorsal arc enclosing the nuchal organ and

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Table 1. Summary of characters in sipunculan genera

S = Sipunculidea form; P = Phascolosomatidea form: see Fig. 1

	Presence of of anal shield	Type of tentacle arrangement	Type of introvert hook when present	Presence of banding in longitudinal muscle layer	Presence of canals or sacs in body wall	Number of retractor muscles apparent	Spindle muscle attached posteriorly	Number of nephridia	Presence of villi on contractile vessel	Number of species
Sipunculus	–	S	—	+[1]	+	4	–	2	–	10
Xenosiphon	–	S	—	+[1]	+	4	–	2	–	1
Siphonosoma	–	S	S	+[1]	+	4	+	2	+/–[7]	10
Siphonomecus	–	S	S	+[1]	+	2	+	2	–	1
Phascolopsis	–	S	—	+	–	4	–	2	–	1
Golfingia	–	S	S	–	–	4	–	2	–	12
Nephasoma	–	S	S	–	–	2	–	2	–	23
Thysanocardia	–	S	—	–	–	2	–	2	+	3
Phascolion	–	S	S	–	–	4[3]	–[5]	1	–[8]	25
Onchnesoma	–	S	—	–	–	2[4]	–[5]	1	–	4
Themiste	–	(S)	S	–	–	2	–	2	+	25
Apionsoma	–	P	P	–	–	4	+	2	–	6
Phascolosoma	–	P	P	+	–	4	+[6]	2	–	36
Antillesoma	–	P	—	+	–	4	+	2	+	1
Aspidosiphon	+	P	P	–/+[2]	–	2	+	2	–	45
Cloeosiphon	+	P	P	–	–	2	+	2	–	1
Lithacrosiphon	+	P	P	+	–	2	+	2	–	2

[1] Circular muscle layer also banded. [2] Present in *A. (Paraspidosiphon)*. [3] Often strongly fused so that number appears to be fewer (3, 2 or 1). [4] Column is entire but thought to be composed of two fused muscles. [5] Spindle muscle absent. [6] Unattached posteriorly in *P. pectinatum*. [7] Absent in some species. [8] Present in *P. cirratum*.

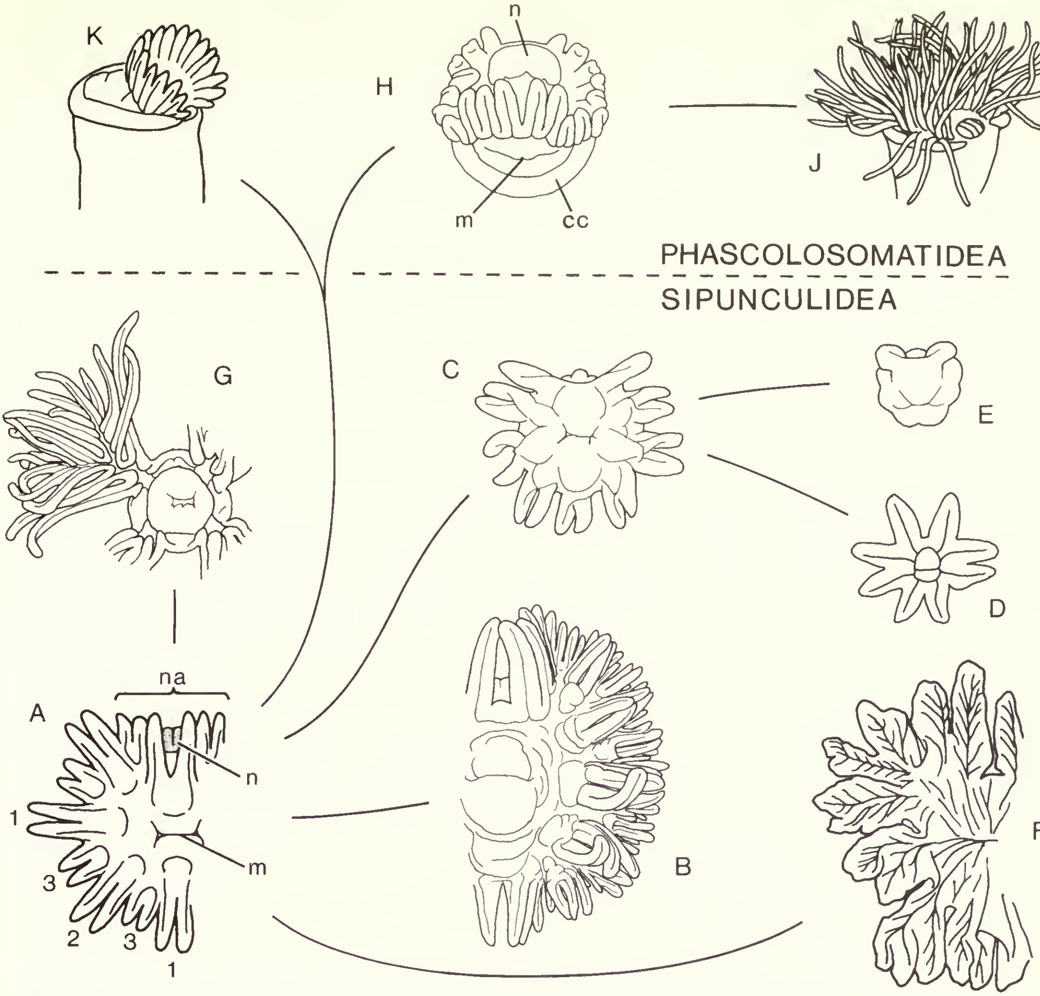

Fig. 1. The structure of the tentacular crown of Sipuncula: some examples illustrating the form and variation within the classes Sipunculidea and Phascolosomatidea. Solid lines indicate possible evolutionary trends. A. Generalised Sipunculidea crown such as might have been possessed by ancestral stock adults; B. *Golfingia margaritacea*; C. *Nephasoma rimicola*; D. *Onchnesoma squamatum*; E. *Nephasoma minutum*; F. *Sipunculus norvegicus*; G. *Themiste lageniformis*; H. *Phascolosoma granulatum*; J. *Antillesoma antillarum*; K. *Aspidosiphon johnstoni*. (B, E, F: after Théel, 1905.) Abbreviations: cc, cephalic collar; m, mouth; n, nuchal organ; na, dorsal arc of tentacles enclosing nuchal organ; 1,2,3, primary, secondary and tertiary tentacle pairs around disk periphery. (Modified from Cutler & Gibbs, 1985.)

there are no peripheral tentacles (Fig. 1). Thus, the two patterns have a common, perhaps homologous, feature in the dorsal arc of tentacles. In evolutionary terms, the peripheral tentacles could be interpreted as a later addition, i.e. the Sipunculidea have evolved from a Phascolosomatidea stock. However, around the margin of the oral disk in Phascolosomatidea there is a prominent ridge, the cephalic collar, and it is thought that this ridge represents a vestige of the peripheral system. If this interpretation is correct the common ancestor must have possessed a Sipunculidea-type of tentacular crown, probably a simple form, somewhat similar to that of *Thysanocardia procera* (Gibbs, Cutler & Cutler, 1983, Fig. 2B), and the peripheral tentacles were lost during an early divergence to give the Phascolosomatidea line. The Sipunculidea tentacular pattern, peripheral circle plus nuchal arc, can perhaps be best regarded as an elaboration of simple prostomial tentacles possessed by the early protostomial stock.

The development of the tentacular crown in the Sipunculidea, as seen for example in *Golfingia* species, commences with the formation of four primary pairs of tentacles in the dorsal, ventral and lateral positions, between which secondary pairs subsequently develop to form a single ring encircling the central mouth on the oral disk (Fig. 1A). Between these pairs tertiary pairs usually develop: in the adult these may be few or very numerous; in the latter case the tentacles are accommodated in loops or 'festoons' that extend aborally on to the anterior introvert. The nuchal organ situated dorsally between the two primary tentacles thus becomes enclosed by an arc of tentacles. As a general rule, the number of tentacles increases with increasing size and age of individuals and large-sized species have more tentacles than small-sized species.

Within the class Sipunculidea a wide range of tentacular development is found. The most highly evolved crown is found in the genus *Thysanocardia,* adult specimens of which often possess well-developed festoons comprising several hundred tentacles; in some *Thysanocardia nigra* (Ikeda) the number exceeds 500 (see Gibbs, Cutler & Cutler, 1983). Large *Golfingia margaritacea* (Sars) have 100 or more tentacles (Fig. 1B) but most other Sipunculidea have around 50 or fewer with only a limited number of tertiary tentacles developing, as in *Golfingia elongata* (Keferstein) with 20–34 and *Nephasoma rimicola* (Gibbs) with 12–20 (Fig. 1C; see Gibbs, 1973). In some species only the primary tentacles appear, as in *Onchnesoma squamatum* (Kor. & Dan.) with 8 and *Nephasoma minutum* (Keferstein) with just two (Fig. 1D, E). Thus the evolution of the tentacular crown could have been not only towards greater complexity but also towards simplification, a trend, possibly neotenous, seen in several genera, notably *Nephasoma* (e.g. *N. minutum*), *Onchnesoma* (e.g. *O. steenstrupi* Kor. & Dan.) and *Phascolion* (e.g. *P. pacificum* Murina). Another variation is seen in some members of the family Sipunculidae where the peripheral tentacles have become flattened and fused to form a continuous veil-like structure, as for example in *Sipunculus norvegicus* Dan. (Fig. 1F). The crown of *Themiste* with its tentacles arising from 4–8 stems appears anomalous at first sight but, in fact, this type represents yet another modification of the basic Sipunculidea pattern. In themistids the secondary tentacles develop between the primary pairs but are borne on outgrowths of the oral disk so that with subsequent tertiary tentacle development, an erect dendritic structure results rather than the typical festoon which is contiguous with the introvert wall. In the themistid type the dorsal primary tentacles are widely spaced and do not enclose the nuchal organ (Fig. 1G).

All six genera grouped in the class Phascolosomatidea are rather similar in terms of the tentacular arrangement: with one exception, all have a single arc of up to 30 tentacles enclosing the nuchal organ (Fig. 1H,K). The exception is *Antillesoma antillarum* (Grube & Oersted) in which the tentacles are fairly numerous (Fig. 1J) presumably as a result of secondary proliferation.

One other character that separates the Sipunculidea and Phascolosomidea is the structure of the introvert hooks on the anterior introvert, when present. In the former group these hooks are somewhat variable but generally are simple, sharply-pointed protrusions of the epidermis and scattered in their distribution; however, in the latter they have a typical recurved shape, usually an internal structure is apparent and they are closely-packed in distinct rings encircling the anterior introvert.

Definitions of orders, families and genera are given below. Four orders are recognised. In the class Sipunculidea, members of the order Sipunculiformes are distinguished by the presence of banding in the longitudinal muscle of the body wall found in five genera, all of which are placed in the family Sipunculidae. The remaining six genera within this class all have a uniform, continuous layer of longitudinal muscle tissue and form the order Golfingiiformes comprising three families — Golfingiidae, Phascolionidae and Themistidae. In the class Phascolosomatidea the genera are separated into two orders, each with a single family, on the basis of the presence (Aspidosiphoniformes: Aspidosiphonidae) or absence (Phascolosomatiformes: Phascolosomatidae) of an anal shield, a hardened thickening of the anterior trunk region. It should be noted that the structure of the anal shield is different in all three genera within the Aspidosiphonidae and it is recognised that this character may have evolved several times.

Whilst the forms of the tentacle crown and of the introvert hooks are useful characters for dividing the 17 genera into two natural groups, here designated as classes, few other major characters are confined to one or other of these two classes (Table 1): coelomic spaces in the body wall is a feature exclusive to Sipunculidae and likewise for anal shield development in Aspidosiphonidae. Other characters are found in both classes, notably the banding of the longitudinal muscle layer in the body wall, the attachment of the spindle muscle to the posterior trunk and an increase in the volume of the contractile vessel through the development of villi in conjunction with increased tentacular volume or area. Such characters would appear to be polyphyletic in origin. There is little doubt that the basic number of introvert retractor muscles is four, arranged as dorsal and ventral pairs. Loss of the dorsal pair appears to have occurred independently in a number of generic lines. Assessing the number of retractors in any one specimen can often be problematical because fusion frequently occurs but may not be evident. In some species only one retractor is apparent in the adult form: in *Phascolion* species there is good evidence to suggest the one muscle is the result of the fusion of all four muscles (Gibbs, 1985) whilst in *Onchnesoma* the single muscle is thought to comprise only the fused ventral pair, the dorsal pair having been lost. Use of the number of retractors as a taxonomic character has to be approached with some caution since even within a single population the number is liable to variation, as noted for *Golfingia elongata* (Gibbs, 1973). Morphological variation seems to be one of the hallmarks of the phylum, a feature that may account for the survival of this small group but one that does not facilitate good taxonomy.

The present scheme of classification (Table 2) updates that given in Stephen & Edmonds (1972) and some later authors by incorporating the recent revisions of several major genera, notably, *Siphonosoma, Golfingia* and *Phascolosoma*. Synonymies are as given in Stephen & Edmonds (1972): any more recent changes are noted under each genus.

Key to Families

1	Tentacles arranged in an arc encircling dorsal nuchal organ; peripheral tentacles absent; hooks complex, in distinct rings [Class ***PHASCOLOSOMATIDEA***]	2
	Tentacles arranged peripherally on oral disk so as to encircle central mouth; may be borne on stem-like outgrowths of oral disk or reduced in number to a single dorsal pair; hooks simple, usually scattered [Class ***SIPUNCULIDEA***]	3
2	Anal shield present	Fam. ***ASPIDOSIPHONIDAE*** (p. 55)
	Anal shield absent	Fam. ***PHASCOLOSOMATIDAE*** (p. 54)
3	Longitudinal muscles of body wall gathered into separate or anastomosing bands	Fam. ***SIPUNCULIDAE*** (p. 48)
	Longitudinal muscle of body wall in a uniform continuous layer	4
4	Tentacles carried on 4–8 stem-like outgrowths of oral disk	Fam. ***THEMISTIDAE*** (p. 53)
	Tentacles not carried on disk outgrowths	5
5	A single nephridium present	Fam. ***PHASCOLIONIDAE*** (p. 51)
	Two nephridia present	Fam. ***GOLFINGIIDAE*** (p. 50)

Classification

Phylum ***SIPUNCULA***
Class ***SIPUNCULIDEA***

Sipuncula with tentacles encircling a central mouth on the oral disk. Introvert hooks (when present) simple, thorn-like hollow structures that are usually irregularly distributed. Spindle muscle unattached posteriorly (except in *Siphonosoma* and *Siphonomecus*).

Order ***SIPUNCULIFORMES***

Sipunculidea with longitudinal muscle in body wall gathered into bands (likewise for circular muscle in two genera—*Sipunculus* and *Xenosiphon*). Coelomic extensions – canals or sacs – in body wall (except in *Phascolopsis*).

Table 2. Classification of the phylum Sipuncula

- Cl. **Sipunculidea**
  - Ord. SIPUNCULIFORMES
    - Fam. SIPUNCULIDAE Stephen & Edmonds, 1972
      - *Sipunculus* Linnaeus, 1766
        - *S. (Sipunculus)*
        - *S. (Austrosiphon)* Fisher, 1954
      - *Xenosiphon* Fisher, 1947
      - *Siphonosoma* Spengel, 1912
      - *Siphonomecus* Fisher, 1947
      - *Phascolopsis* Fisher, 1950
  - Ord. GOLFINGIIFORMES
    - Fam. GOLFINGIIDAE Stephen & Edmonds, 1972
      - *Golfingia* Lankester, 1885
      - *Nephasoma* Pergament, 1946
      - *Thysanocardia* Fisher, 1950
    - Fam. PHASCOLIONIDAE Cutler & Gibbs, 1985
      - *Phascolion* Théel, 1875
        - *P. (Phascolion)*
        - *P. (Isomya)* Cutler & Cutler, 1985
        - *P. (Montuga)* Gibbs, 1985
        - *P. (Lesenka)* Gibbs, 1985
        - *P. (Villiophora)* Cutler & Cutler, 1985
      - *Onchnesoma* Koren & Danielssen, 1875
    - Fam. THEMISTIDAE Cutler & Gibbs, 1985
      - *Themiste* Gray, 1828
        - *T. (Themiste)*
        - *T. (Lagenopsis)* Edmonds, 1980
- Cl. **Phascolosomatidea**
  - Ord. PHASCOLOSOMATIFORMES
    - Fam. PHASCOLOSOMATIDAE Stephen & Edmonds, 1972
      - *Phascolosoma* Leuckart, 1828
        - *P. (Phascolosoma)*
        - *P. (Edmondsius)* subgen. nov.
      - *Apionsoma* Sluiter, 1902
      - *Antillesoma* Stephen & Edmonds, 1972
  - Ord. ASPIDOSIPHONIFORMES
    - Fam. ASPIDOSIPHONIDAE Baird, 1868
      - *Aspidosiphon* Diesing, 1851
        - *A. (Aspidosiphon)*
        - *A. (Paraspidosiphon)* Stephen, 1964
      - *Cloeosiphon* Grube, 1868
      - *Lithacrosiphon* Shipley, 1902

Family *SIPUNCULIDAE* Baird, 1868

Characters are those of the order.

Key to Genera

1	Body wall circular muscle layer continuous	***PHASCOLOPSIS***
	Body wall circular muscle layer gathered into bands	2
2	Body wall circular and longitudinal muscle bands anastomosing, spindle muscle attached to posterior end of trunk	3
	Body wall circular and longitudinal muscle bands not anastomosing, spindle muscle not attached to posterior trunk.	4
3	Four introvert retractor muscles	***SIPHONOSOMA***
	Two introvert retractor muscles	***SIPHONOMECUS***

4 Gut with post-oesophageal loop; coelom extends into body wall as longitudinal canals running throughout most of trunk length . . . .*SIPUNCULUS*

Gut without post-oesophageal loop; coelom extends into body wall as short diagonal canals running across the width of one circular muscle band . . . . *XENOSIPHON*

Genus *SIPUNCULUS* Linnaeus, 1766

DIAGNOSIS. Introvert much shorter than trunk, without hooks, covered with scattered subtriangular papillae. Trunk cylindrical. Body wall contains coelomic extensions in the form of parallel longitudinal canals which extend most of trunk length. Circular and longitudinal muscle layers gathered into distinct bands. Oral disk carries tentacles arranged around the mouth sometimes modified with the development of an inter-tentacular membrane (*S. nudus* L., *S. norvegicus* Danielssen). Four introvert retractor muscles. Two protractor muscles may be developed (*S. mundanus* Sel. & Bülow). Two contractile vessels, both without villi. Gut with post-oesophageal loop, caecum on rectum, and coil attached to body wall along its entire length by many connective strands. Spindle muscle not attached posteriorly. Two nephridia. Species usually large-sized (trunk greater than 5 cm long in adults).

TYPE SPECIES. *Sipunculus nudus* Linnaeus, 1766, subsequent designation, ?Fisher 1952.

Subgenus *SIPUNCULUS* Linnaeus, 1766

Sipunculus (Sipunculus): Cutler & Cutler, 1985*a*: 232.

DIAGNOSIS. Nephridia anterior to anus. Spindle muscle originates on body wall anterior to anus.

TYPE SPECIES. *Sipunculus nudus* Linnaeus, 1766, subsequent designation, ?Fisher, 1952.

Subgenus *AUSTROSIPHON* Fisher, 1954, emended

Xenosiphon (Austrosiphon) Fisher, 1954: 314.
Xenosiphon (Xenopsis) Johnson, 1969: 44.
Sipunculus (Contraporus) Cutler & Cutler, 1985*a*: 241.

DIAGNOSIS. Nephridia posterior to anus. Spindle muscle originates from ventral surface of rectum.

TYPE SPECIES. *Sipunculus mundanus* Selenka & Bülow, 1883, monotypy.

Genus *XENOSIPHON* Fisher, 1947

DIAGNOSIS. Introvert much shorter than trunk, and without hooks but covered with scattered subtriangular papillae. Body wall contains coelomic extensions in form of short, diagonal canals limited in length to width of one circular muscle band. Circular and longitudinal muscle layers divided into distinct bands. Oral disk carries tentacles arranged around mouth. Four introvert retractor muscles and two thin protractor muscles present. Contractile vessel without villi, gut without post-oesophageal loop, caecum present on rectum and coil attached to body wall along entire length by connective strands. Spindle muscle originates on ventral wall of rectum and is not attached to the body wall posteriorly. Anus anterior to nephridiopores. Two nephridia. Contains one large-sized species.

TYPE SPECIES. *Sipunculus mundanus* var. *branchiatus* Fischer, 1895, original designation.

REMARKS. The two subgenera previously included in this genus are now assigned to *Sipunculus* (see above).

Genus *SIPHONOSOMA* Spengel, 1912

Siphonosoma (Siphonosoma): Fisher, 1950b: 805.
Siphonosoma (Hesperosiphon) Fisher, 1950b: 805.
Siphonosoma (Dasmosiphon) Fisher, 1950b: 805.

DIAGNOSIS. Introvert much shorter than the trunk with prominent conical papillae (sometimes also hooks) arranged in rings. Body wall with coelomic sac-like extensions; circular and longitudinal muscle layers gathered into anastomosing bands. Oral disk carries tentacles arranged around the mouth. Four introvert retractor muscles. Contractile vessel with or without villi. Spindle muscle attached posteriorly. Two nephridia. Species usually large-sized (trunk greater than 5 cm long in adults).

TYPE SPECIES. *Phascolosoma australe* Keferstein, 1865, subsequent designation, Gerould, 1913.

REMARKS. The three subgenera recognised by Fisher (1950b) were distinguished by the presence or absence of transverse dissepiments and rectal caeca. These characters have been found to be subject to great variation and of limited diagnostic value: consequently, this subgeneric separation is not supportable (Cutler & Cutler, 1982).

Genus *SIPHONOMECUS* Fisher, 1947

DIAGNOSIS. Introvert much shorter than trunk with prominent hooks and conical papillae arranged in rings. Body wall with coelomic extensions (sacs); circular and longitudinal muscle layers gathered into anastomosing bands. Oral disk carries tentacles arranged around the mouth. Two introvert retractor muscles. Contractile vessel without villi. Spindle muscle attached posteriorly. Two nephridia. Contains one large-sized species.

TYPE SPECIES. *Siphonomecus multicinctus* Fisher, 1947, original designation.

Genus *PHASCOLOPSIS* Fisher, 1950

DIAGNOSIS. Introvert shorter than trunk with deciduous hooks (present in juvenile but lost in adult). Body wall without coelomic extensions. Circular muscle layer continuous, longitudinal muscle layer gathered into anastomosing bands. Oral disk carries tentacles arranged around the mouth. Four introvert retractor muscles. Contractile vessel without villi. Spindle muscle not attached posteriorly. Two nephridia. Contains one large-sized species.

TYPE SPECIES. *Sipunculus gouldii* Portalès, 1851, monotypy.

Order **GOLFINGIIFORMES**

Sipunculidea with body wall longitudinal muscle in a continuous layer, not gathered in bands.

Family **GOLFINGIIDAE** Stephen & Edmonds, 1972

Golfingiiformes with two nephridia. Tentacles not borne on stem-like extensions of oral disk.

Key to Genera

1	Contractile vessel with numerous villi	***THYSANOCARDIA***
	Contractile vessel without villi	2
2	Four introvert retractor muscles	***GOLFINGIA***
	Two introvert retractor muscles	***NEPHASOMA***

Genus *GOLFINGIA* Lankester, 1885

Golfingia (Golfingia): Fisher, 1950a; 549.
Golfingia (Dushana) Murina, 1975: 1085.
Themiste (Stephensonum) Edmonds, 1980: 33.
Centrosiphon Shipley, 1903: 173.

DIAGNOSIS. Introvert about equal to or shorter than trunk; hooks when present are usually scattered (arranged in rings in *G. elongata*). Body wall with continuous muscle layers. Oral disk carries tentacles arranged around the mouth. Four introvert retractor muscles. Contractile vessel without villi. Spindle muscle not attached posteriorly. Two nephridia. Species small- to large-sized.

TYPE SPECIES. *Golfingia macintoshii* Lankester, 1885 [=*Sipunculus vulgaris* de Blainville, 1827: Stephen, 1934], monotypy.

Remarks. This genus now contains only those species previously assigned to the nominate subgenus *Golfingia (Golfingia)*. It includes *Centrosiphon* Shipley, 1903: Edmonds (1980) placed the type species *C. herdmani* Shipley within the genus *Golfingia*; the *Centrosiphon* specimens recorded by Cutler & Cutler (1979) are now considered to be aberrant *Aspidosiphon*.

The subgenus *G. (Dushana)* Murina, 1975, was characterised by complete or partial fusion of the dorsal and ventral retractor muscles on one side of the body. However, it is known that such fusion of the retractors, and also reduction of the retractor number through loss of one or both dorsal retractors, are features of some *Golfingia* species, for example *G. elongata* (see Gibbs, 1973). The holotype of *G. (Dushana) adriatica* Murina shows a similar retractor arrangement (Murina, 1975, Fig. 1) to that described by Watier (1932) for aberrant *G. vulgaris*. The type species originally designated for *G. (Dushana)*, *G. scutiger* (Roule), does not differ significantly in its retractor arrangement (Roule, 1906, Fig. 95) from typical *Golfingia* species. Thus *G. (Dushana)* is no longer recognised.

Genus *NEPHASOMA* Pergament, 1946

Golfingia (Phascoloides) Fisher, 1950a: 550.

Diagnosis. Introvert about equal to, or shorter than, trunk. Hooks when present usually scattered (arranged in rings in *N. rimicola* (Gibbs), in spirals in *N. abyssorum* (Kor. & Dan.)). Body wall with continuous muscle layers. Oral disk carries tentacles arranged around the mouth but tentacles may be reduced in both size and number and restricted to dorsal region. Two introvert retractor muscles often partially fused. Contractile vessel without villi. Spindle muscle not attached posteriorly. Two nephridia. Species generally small- to medium-sized (trunk less than 5 cm in length).

Type species. *Nephasoma marinki* Pergament, 1946 [= *Onchnesoma glaciale* Danielssen & Koren: Cutler & Murina, 1977; = *Phascolosoma lilljeborgii* Danielssen & Koren: Gibbs, 1982], monotypy.

Remarks. This genus now contains all those species previously assigned to the *Golfingia* subgenus *Phascoloides* Fisher, 1950, since *Nephasoma* Pergament has been shown to have priority over *Phascoloides* (Cutler & Murina, 1977).

Genus *THYSANOCARDIA* Fisher, 1950

Diagnosis. Introvert longer than trunk, without hooks. Body wall with continuous muscle layers. Oral disk carries tentacles arranged around the mouth; those enclosing nuchal organ are well developed. Two introvert retractor muscles. Contractile vessel with distinct villi. Spindle muscle not attached posteriorly. Two nephridia. Species small- to medium-sized (adults generally under 5 cm in trunk length).

Type species. *Phascolosoma procerum* Möbius, 1875, original designation.

Remarks. The subgenus *Golfingia (Thysanocardia)* was recently elevated to generic rank and the number of species reduced to three by Gibbs, Cutler & Cutler (1983).

Family **PHASCOLIONIDAE** Cutler & Gibbs, 1985

Golfingiiformes with one nephridium (usually the right). Tentacles not borne on stem-like extensions of oral disk. Gut coil without well-defined axial spindle muscle.

Key to Genera

1 Anus usually situated on anterior trunk; epidermal 'holdfast' or 'attachment' papillae often present. Retractor muscles highly fused but usually 2–4 roots apparent at base of column . . . . *PHASCOLION*

Anus situated on distal half of introvert; epidermal 'attachment' papillae absent. Retractor muscle(s) appear as single column without separate roots . . . . *ONCHNESOMA*

Genus *PHASCOLION* Théel, 1875

DIAGNOSIS. Introvert length one-half to four times that of trunk length, with or without hooks. Trunk usually with modified 'holdfast' papillae. Body wall with continuous muscle layers. Oral disk carries tentacles arranged around the mouth. Introvert retractor muscle system modified by fusion of dorsal and ventral pairs: relative size and degree of fusion defines subgenera (see below). Contractile vessel without villi (but present in *P. cirratum*). Gut coiling generally loose and without axial spindle muscle. One nephridium (usually right). Species small- to medium-sized (less than 5 cm in length) generally inhabiting mollusc shells.

TYPE SPECIES. *Sipunculus strombus* Montagu, 1804, monotypy.

Subgenus *PHASCOLION* Théel, 1875

Phascolion (Phascolion): Gibbs, 1985: 314.

DIAGNOSIS. Retractor column divided for most of its length: oesophagus detaches from retractor column at a point posterior to the first separation of the retractor muscles. Dorsal retractor(s) much more strongly developed than ventral retractor(s). Contractile vessel without villi.

TYPE SPECIES. *Sipunculus strombus* Montagu, 1804, monotypy.

Subgenus *ISOMYA* Cutler & Cutler, 1985

Phascolion (Isomya) Cutler & Cutler 1985*b*: 820

DIAGNOSIS. Characters as for *P. (Phascolion)* except that dorsal and ventral retractor muscles are about equal in diameter.

TYPE SPECIES. *Phascolion tuberculosum* Théel, 1875, original designation.

Subgenus *MONTUGA* Gibbs, 1985

Phascolion (Montuga) Gibbs, 1985: 315.

DIAGNOSIS. Retractor column divided only at posterior end: oesophagus detaches from retractor column at a point anterior to the first separation of the retractor muscles. Contractile vessel without villi.

TYPE SPECIES. *Phascolion lutense* Selenka, 1885, original designation.

Subgenus *LESENKA* Gibbs, 1985

Phascolion (Lesenka) Gibbs, 1985: 315.

DIAGNOSIS. Retractor column entire with retractor muscles fused throughout whole length. Contractile vessel without villi.

TYPE SPECIES. *Phascolion cryptum* Hendrix, 1975, original designation.

Subgenus *VILLIOPHORA* Cutler & Cutler, 1985

Phascolion (Villiophora) Cutler & Cutler, 1985*b*: 821.

DIAGNOSIS. Retractor column entire with retractor muscles fused throughout whole length. Contractile vessel with numerous villi.

TYPE SPECIES. *Phascolion cirratum* Murina, 1968, monotypy.

Genus *ONCHNESOMA* Koren & Danielssen, 1875

DIAGNOSIS. Introvert much longer than trunk. Body wall with continuous muscle layers. Oral disk carries tentacles arranged around mouth but tentacles may be highly reduced in size. Introvert retractor muscle system modified by fusion to form single retractor muscle. Anus situated on introvert. Contractile vessel rarely apparent and without villi. Spindle muscle absent. One nephridium (right). Species small-sized (trunk less than 1 cm in length).

TYPE SPECIES. *Onchnesoma steenstrupii* Koren & Danielssen, 1875, subsequent designation, Stephen & Edmonds, 1972.

Family **THEMISTIDAE** Cutler & Gibbs, 1985

Golfingiiformes with two nephridia. Tentacles borne on stem-like extensions of oral disk.

Genus ***THEMISTE*** Gray, 1828

DIAGNOSIS. Introvert less than trunk length. Body wall with continuous muscle layers. Oral disk carries tentacles basically surrounding mouth but extending with growth along margins of stem-like outgrowths of the oral disk. With or without hooks. Two introvert retractor muscles. Contractile vessel with villi. Spindle muscle not attached posteriorly. Two nephridia. Species small- to large-sized.

TYPE SPECIES. *Themiste hennahi* Gray, 1824, monotypy.

Subgenus ***THEMISTE*** Gray, 1828

Themiste (Themiste): Edmonds, 1980: 33.

DIAGNOSIS. Contractile vessel with long, thread-like villi.

TYPE SPECIES. *Themiste hennahi* Gray, 1828, monotypy.

Subgenus ***LAGENOPSIS*** Edmonds, 1980

Themiste (Lagenopsis) Edmonds, 1980: 33.

DIAGNOSIS. Contractile vessel with short, digitiform villi.

TYPE SPECIES. *Themiste lageniformis* Baird, 1868, original designation.

REMARKS. The subgenus *T. (Stephensonum)* Edmonds, 1980, was erected to include two species of *Themiste* having four, not two, retractor muscles, namely, *Themiste stephensoni* (the type species, original designation) and *T. pinnifolia*. The type material of *Themiste stephensoni* (Stephen) (described under the name *Dendrostomum* Grube, a junior synomym) in the RSME collections has been examined. The holotype (1958.23.24) has a golfingiid, not themistid, tentacle crown (as shown by dissection of the introvert) and the 'band of very short villi' on the contractile vessel (Stephen, 1942, p. 252) do not appear to be true villi but rather outpoutchings of a relatively voluminous vessel. The specimen is clearly a *Golfingia* and probably *G. capensis* (Teuscher); the other type specimens comprise further *Golfingia* but also include some *Themiste* all of which have the typical number of retractors (two). Thus *T. (Stephensonum)* becomes a junior synonym of *Golfingia*. The species *Themiste pinnifolia* (Keferstein) is based on a single specimen, collected more than 100 years ago, which cannot be traced. No subsequent record appears in the literature, despite extensive collecting in the area of the type locality (St Thomas, West Indies). Since the generic identity of this specimen is in doubt, the species name *pinnifolia* is regarded as a *nomen dubium*.

Class **PHASCOLOSOMATIDEA**

Sipuncula with tentacles confined to an arc enclosing dorsal nuchal organ: peripheral tentacles absent. Introvert hooks recurved, usually with an internal structure and closely-packed in regularly-spaced rings (absent in *Antillesoma*). Spindle muscle attached posteriorly.

Order **PHASCOLOSOMATIFORMES**

Phascolosomatidea with anterior trunk not modified to form anal shield. Four introvert retractor muscles.

Family **PHASCOLOSOMATIDAE** Stephen & Edmonds, 1972

Characters are those of the order.

Key to Genera

1	Introvert hooks absent. Contractile vessel with villi	***ANTILLESOMA***
	Introvert hooks present. Contractile vessel without villi	2
2	Longitudinal muscle in body wall gathered into bands	***PHASCOLOSOMA***
	Longitudinal muscle in body wall a uniform continuous layer	***APIONSOMA***

Genus ***PHASCOLOSOMA*** Leuckart, 1828

Diagnosis. Introvert variable in length, often equal to trunk with numerous rings of recurved hooks (absent in *P. meteori* Hérubel). Body wall with longitudinal muscle layer gathered into bands. Oral disk carries relatively few tentacles (less than 30) enclosing nuchal organ. Contractile vessel without true villi (may have bulbous vesicles). Four introvert retractor muscles; lateral pairs sometimes partially, rarely completely, fused. Spindle muscle attached posteriorly (except in *P. pectinatum*). Two nephridia.

Type species. *Phascolosoma granulatum* Leuckart, 1828, monotypy.

Subgenus ***PHASCOLOSOMA*** Leuckart, 1828

Phascolosoma (Phascolosoma): Stephen & Edmonds, 1972: 289.
?Phascolosoma (Rueppellisoma) Stephen & Edmonds, 1972: 271.
?Phascolosoma (Satonus) Stephen & Edmonds, 1972: 28 (in part).

Diagnosis. Spindle muscle attached posteriorly. Introvert hook without accessory spinelets.

Type species. *Phascolosoma granulatum* Leuckart, 1828, monotypy.

Subgenus ***EDMONDSIUS*** subgen. nov.

Phascolosoma (Satonus) Stephen & Edmonds, 1972: 282 (in part)

Diagnosis. Spindle muscle not attached posteriorly. Introvert hook with accessory spinelets at base.

Type species. *Phascolosoma pectinatum* Keferstein, 1867, monotypy.
The subgenus is named in honour of Dr Stanley J. Edmonds.

Remarks. Stephen & Edmonds (1972) attempted to divide this large genus by creating four subgenera, *P. (Phascolosoma)*, *P. (Rueppellisoma)*, *P. (Antillesoma)* and *P. (Satonus)*, for the most part using published descriptions concerning the number of retractor muscles (four or two), presence or absence of contractile vessel villi and whether or not the spindle muscle is attached posteriorly. In examining all of the available type material, Cutler & Cutler (1983) found that the subgeneric distinctions were highly confused because many of the original descriptions contained errors. *P. (Rueppellisoma)*, comprising eight putative species each allegedly with two retractor muscles, is now considered invalid (all *Phascolosoma* are now interpreted as having four retractors), the type species, *Phascolosoma rueppellii* Grube, 1868, by original designation, being placed as *incertae sedis* since the type is lost. *P. (Antillesoma)*, formerly containing six species, now contains only the type species, *Phascolosoma antillarum* Grube & Oersted, 1858, original designation; this subgenus is sufficiently distinct as to warrant generic rank (see below). The remaining subgenus, *P. (Satonus)*, is distinguished from the nominate subgenus by the absence of a posterior attachment of the spindle muscle. This character is difficult to determine with any degree of certainty in any specimen that has been damaged internally, become macerated or has dried, as found when most of the type materials of the eight species grouped in *P. (Satonus)* were re-examined, including that of the type species, *Phymosoma nigritorquatum* Sluiter, 1882, original designation. Just one species, *Phascolosoma pectinatum* Keferstein, 1867, appears to fit the definition of *P. (Satonus)*. Since the type species of this subgenus, *P. nigritorquatum*, has uncertain status (it may be a junior synonym of *P. (Phascolosoma) scolops* (Selenka & de Man)), it has been categorised as *incertae sedis* (Cutler & Cutler, 1983). Thus *P. (Satonus)* is invalid and the new subgenus accommodates *P. pectinatum.*

Genus *APIONSOMA* Sluiter, 1902

Apionsoma Sluiter, 1902: 42.
Golfingia (Mitosiphon) Fisher, 1950a: 550.
Golfingia (Phascolana) Wesenberg-Lund, 1959: 183.
Fisherana Stephen, 1964: 460.
Golfingia (Siphonoides) Murina, 1967: 1334.

DIAGNOSIS. Introvert of variable length in relation to trunk with rings of recurved hooks (absent in *A. trichocephala*) that in some species have accessory spinelets at base. Body wall with continuous muscle layers. Oral disk with tentacles enclosing nuchal organ but not mouth. Contractile vessel without villi. Four introvert retractor muscles. Spindle muscle attached posteriorly. Two nephridia, sometimes bilobed. Species small-sized (less than 2 cm in length).

TYPE SPECIES. *Apionsoma trichocephala* Sluiter, 1902, monotypy.

REMARKS. Cutler (1979) reviewed this taxon which is here elevated to generic status. It includes many species previously assigned to various *Golfingia* subgenera and *Fisherana* (see above). This genus is one that still presents problems, in particular, the precise nature of the oral disk in *A. trichocephala* remains unknown. The variations within the genus may justify the use of subgenera.

Genus *ANTILLESOMA* Stephen & Edmonds, 1972

Phascolosoma (Antillesoma) Stephen & Edmonds, 1972: 277.

DIAGNOSIS. Introvert variable in length, often about equal to trunk, without hooks. Body wall with longitudinal muscle layer gathered into anastomosing bands. Oral disk carries numerous tentacles (more than 30 in adults) enclosing nuchal organ. Contractile vessel with many villi. Four introvert retractor muscles, lateral pairs often extensively fused. Spindle muscle attached posteriorly. Two nephridia. Contains one small- to medium-sized species (less than 5 cm in length).

TYPE SPECIES. *Phascolosoma antillarum* Grube & Oersted, 1858, original designation.

REMARKS. This taxon was erected as a subgenus to include six *Phascolosoma* species but is now considered to be monospecific (Cutler & Cutler, 1983) and of generic rank.

Order **ASPIDOSIPHONIFORMES**

Phascolosomatidea with the anterior trunk hardened to form a horny or calcareous anal shield. Two retractor muscles.

Family **ASPIDOSIPHONIDAE** Baird, 1868

Characters are those of the order.

Key to Genera

1 Introvert protrudes from centre of anal shield. Shield calcareous (white) composed of numerous polygonal plates . . . . ***CLOEOSIPHON***
Introvert protrudes from ventral margin of anal shield 2
2 Shield composed of single calcareous cap . . . . ***LITHACROSIPHON***
Shield composed of numerous horny (brown-black) plates. . . . . ***ASPIDOSIPHON***

Genus *ASPIDOSIPHON* Diesing, 1851

DIAGNOSIS. Introvert usually longer than trunk with recurved hooks in numerous rings. Trunk with anal shield composed of hardened plates (occasionally inconspicuously developed). Introvert protrudes from ventral margin of shield. Body wall either with continuous longitudinal muscle layer or with longitudinal muscle layer gathered into anastomosing, sometimes ill-defined, bands. Oral disk with tentacles enclosing nuchal organ but not mouth. Contractile vessel without villi. Two introvert retractor muscles often almost completely fused. Spindle muscle attached posteriorly. Two nephridia. Species small- to medium-sized.

TYPE SPECIES. *Aspidosiphon muelleri* Diesing, 1851, subsequent designation, Stephen & Edmonds, 1972.

Subgenus *ASPIDOSIPHON* Diesing, 1851

Aspidosiphon (Aspidosiphon): Cutler, 1973: 174.

DIAGNOSIS. Longitudinal muscle layer of body wall continuous, not gathered into bands.

TYPE SPECIES. *Aspidosiphon muelleri* Diesing, 1851, subsequent designation, Stephen & Edmonds, 1972.

Subgenus *PARASPIDOSIPHON* Stephen, 1964

Paraspidosiphon Stephen, 1964: 459.
Aspidosiphon (Paraspidosiphon): Cutler, 1973: 168.

DIAGNOSIS. Longitudinal muscle layer of body wall gathered into bands.

TYPE SPECIES. *Aspidosiphon steenstrupii* Diesing, 1859, original designation.

REMARKS. Earlier diagnoses of this genus contain serious errors. The tentacular arrangement is phascolosomatid (Gibbs, 1977; Gibbs, in Edmonds, 1980) and there are always two retractor muscles. Although *A. semperi* ten Broeke and *A. insularis* Lanchester are described as having four retractor muscles, the type of the former (ZMUA collection) has, in fact, two, and the type of the latter (BMNH: Reg. 1924.3.1.80) is not an *Aspidosiphon* but a *Phascolosoma* (possibly *P. perlucens* Baird). In *Aspidosiphon* species the spindle muscle is always attached posteriorly.

Genus *CLOEOSIPHON* Grube, 1868

DIAGNOSIS. Introvert longer than trunk with numerous rings of recurved hooks. Trunk with conspicuous anal shield composed of small rectangular calcareous plates. Introvert protrudes through centre of shield. Body wall with continuous muscle layers. Oral disk carries tentacles enclosing nuchal organ, but not mouth. Contractile vessel without villi. Two introvert retractor muscles often almost completely fused. Spindle muscle attached posteriorly. Two nephridia. Contains one medium-sized species.

TYPE SPECIES. *Loxosiphon aspergillus* Quatrefages, 1865, monotypy.

Genus *LITHACROSIPHON* Shipley, 1902

DIAGNOSIS. Introvert about equal to trunk with numerous rings of recurved hooks. Trunk with anal shield formed by internal calcareous conical structure. Body wall with longitudinal muscle layer gathered into bands. Oral disk with tentacles enclosing nuchal organ but not mouth. Contractile vessel without villi. Two introvert retractor muscles, often almost completely fused. Spindle muscle attached posteriorly. Two nephridia. Species small- to medium-sized (less than 4 cm in length).

TYPE SPECIES. *Lithacrosiphon maldiviense* Shipley, 1902, monotypy.

REMARKS. This genus now contains two species (see Cutler & Cutler, 1981).

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Two new species of *Garra (Teleostei–Cyprinidae)* from the Arabian peninsula

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Introduction

Continued interest in speleology in Oman has led to the discovery of yet another hypogean, but in this case microphthalmic, species of the cyprinid genus *Garra* from an extremely isolated sink hole in the Jabal Qara mountains of Oman. In the course of comparing this new species with its congeners, using the recent revision of Krupp (1983), the discovery of more specimens of Krupp's '*Garra*: incertae sedis (1)' enabled a second new species to be described. In all, eight species of *Garra* are now known from the Arabian peninsula.

Garra dunsirei sp. nov.
(Fig. 1)

The first four specimens received (BMNH 1984.3.6: 577–580) were collected by Mr A. Dunsire and Mr D. Green on 16 May 1980, but were in too poor a condition to be used for description. A further consignment of 19 live specimens (13 of which were still alive at the time of writing, July 1985) was collected by Mr D. Maclelland on 26 February 1983.

HOLOTYPE. BMNH 1984.3.6: 571, 68 mm SL; Tawi Atair (17°06′N, 54°34′E) in the Jabal Qara (variously Jabal Samhan) mountains, Dhofar, Oman.

PARATYPES. BMNH 1984.3.6: 572–576, 34–49 mm, same data as holotype.

LOCALITY. The fishes were caught in a pool in a side passage 200 m down the sink hole shown in Plates 1 and 2. The surface drainage is southwards to the Arabian Sea. The significance of the drainage direction and the isolated of the locality will be discussed below.

DESCRIPTION. The description is based on the holotype and five paratypes (34–68 mm SL), all of which were radiographed. Additionally two of the first four specimens (1984.3.6: 577–580) were cleared and stained with alizarin. All measurements are expressed as a percentage of the standard length. Because the sample is so small, the measurements of the holotype are included in the range as well as being given in parentheses.

MORPHOMETRIC DATA. Body depth $\bar{x}$=22·9, range=21·4–23·8 (23·8); head length, $\bar{x}$=27·3, range=25·0–30·3 (25·0); eye diameter $\bar{x}$=3·3, range=2·8–3·7 (3·7); interorbital width $\bar{x}$=9·4, range=8·2–10·0 (8·8); pectoral fin length $\bar{x}$=20·2, range=18·8–21·4 (19·3); caudal peduncle length $\bar{x}$=13·7, range=12·0–16·0 (14·7); caudal peduncle depth $\bar{x}$=10·1, range=9·2–11·4 (10·3); anterior barbel length $\bar{x}$=4·2, range=3·7–4·5 (3·7); posterior barbel length $\bar{x}$=3·5, range=2·2–4·0 (2·6); dorsal fin height $\bar{x}$=23·1, range=22·2–23·8 (22·8); mental disc maximum length $\bar{x}$=7·4, range=6·5–8·8 (6·5); mental disc maximum width $\bar{x}$=7·3, range=7·1–8·1 (7·2); distance between snout and anus $\bar{x}$=76·6, range=73·5–78·5 (74·4); distance between snout and anal fin origin $\bar{x}$=80·9, range=77·9–83·6 (78·7); distance between snout and pelvic fin origin $\bar{x}$=60·5, range=58·8–63·3 (59·1); distance between snout and dorsal fin origin $\bar{x}$=53·0, range=45·9–55·9 (51·5).

The body shape and details of the mental disc are shown in Figs 1 and 2a. The abdomen of the holotype has collapsed, creating an uncharacteristic flat-bellied appearance. The eyes are very small and not visible in ventral view. The mental disc is approximately circular. In the smallest specimen (34 mm SL), only the posterior margin of the disc is free, but as the fish grows, the rest of

Bull. Br. Mus. nat. Hist. (Zool.) **52**(1): 59–70 Issued 29 January 1987

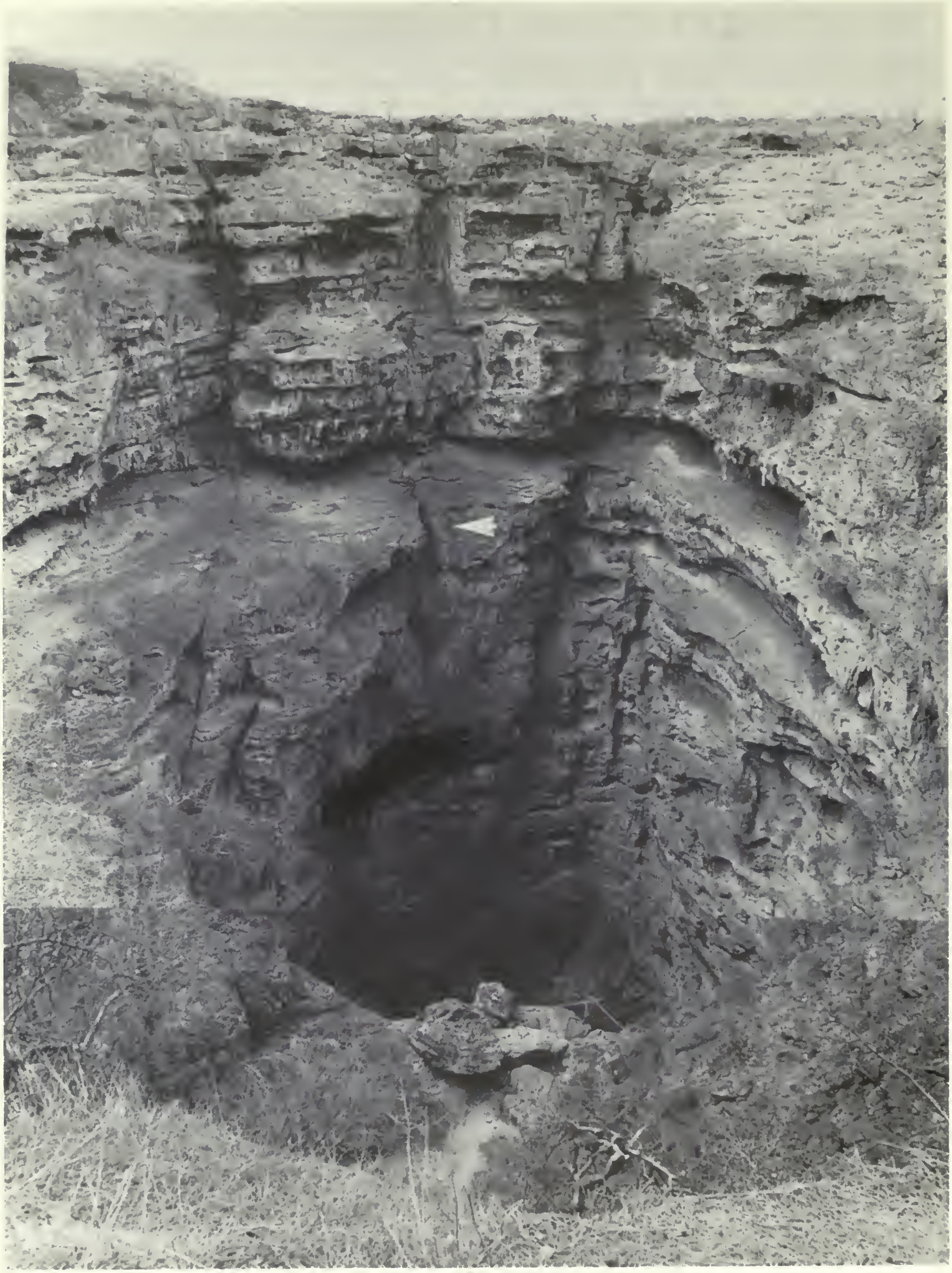

Plate 1. The sink hole at Tawi Atair.

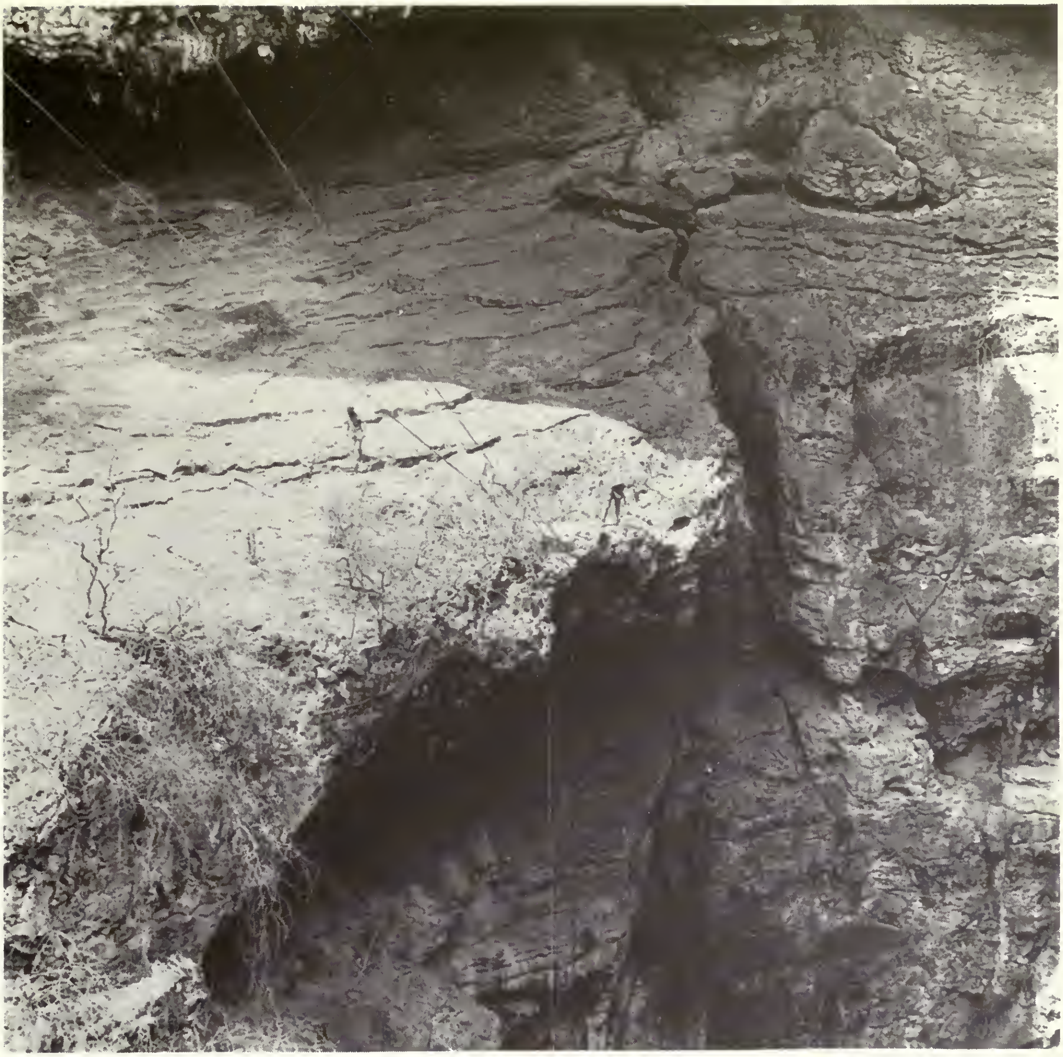

Plate 2. A close-up of the arrowed area in Plate 1 to indicate the size of the sink hole.

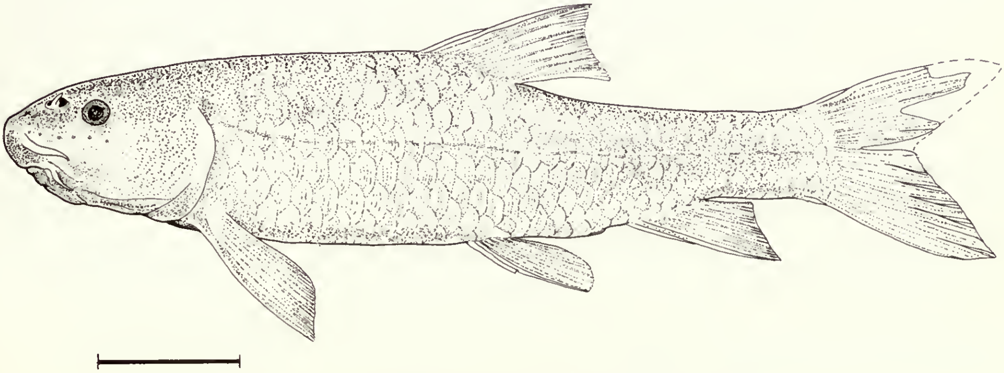

Fig. 1. *Garra dunsirei* Holotype. Scale = 10 mm.

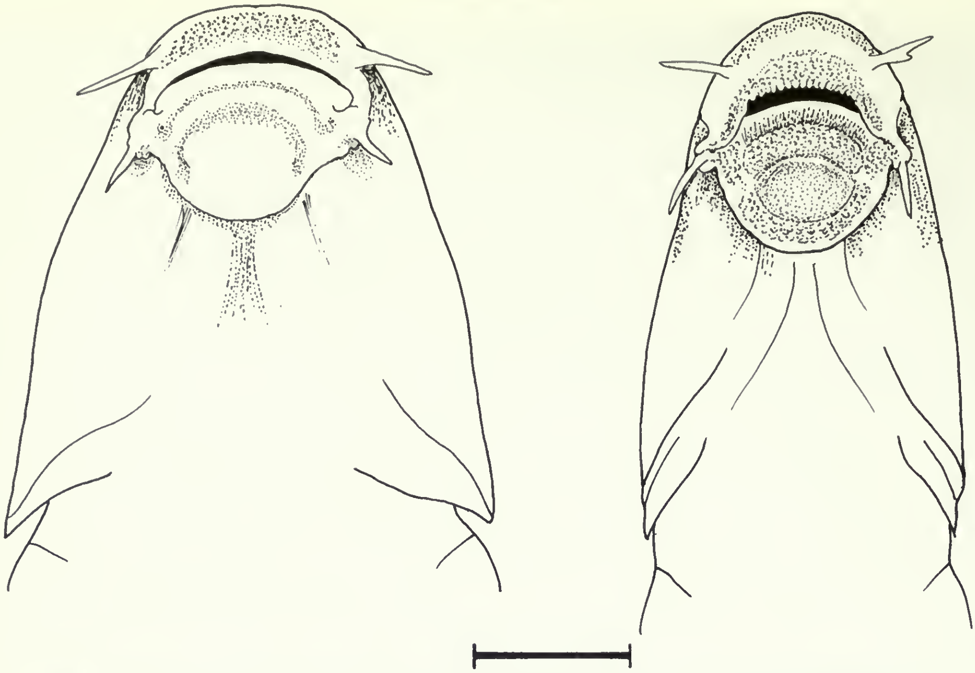

Fig. 2. Ventral views of the heads of a. *Garra dunsirei* and b. *Garra lautior*. Scale = 5 mm.

the rim becomes free. The papillae are scarcely developed, the papillar bed being only just differentiated in a specimen of 50 mm SL (Fig. 2a). Only on the holotype are the papillae well formed. The size and extent of the papillae are less than in all other *Garra* in the region.

None of the specimens, alive or preserved, has tubercles on the snout, although a 39·5 mm SL specimen is a gravid female.

SQUAMATION. The scales are less well developed than those of the hypogean population of *Garra barreimiae* (Banister, 1984) which, although thinner than the scales of epigean populations, are scarcely less extensive. In *Garra dunsirei* the scales are as deep as, or deeper, than long and although they fill the scale pocket vertically, they often fail to reach the posterior edge of the pocket. A scale and its pattern of striations is shown in Fig. 3. Scales of the holotype have eleven 'growth' rings. It is not known if these represent annual or seasonal spawning marks or are the result of growth changes caused by food availability. Food only comes into the cave during the annual rains. The scales of the ventral region of the body are severely reduced or absent. In the lateral line series there are 34(f2), 35(f3) or 36(f1) scales. There are $3\frac{1}{2}$(f6) scale rows from the dorsal fin base to the lateral line and $2\frac{1}{2}$(f3) or $3\frac{1}{2}$(f3) scale rows from there to the pelvic fin base. On the two specimens on which a count was possible there are $6\frac{1}{2}$ scale rows from the lateral line to the ventral mid-line. Twelve (f6) scale rows encircle the least circumference of the caudal peduncle.

VERTEBRAE. Radiographs revealed the presence of 32(f3) or 33(f3) vertebrae, excluding those forming the Weberian mechanism. It was difficult to identify with certainty the first caudal vertebra but there appear to be 18(f2) or 19(f4) abdominal vertebrae. There are 14(f2) or 15(f4) pairs of ribs.

Characteristic of this species is the most unusual change of shape of the neural arches and spines below the dorsal fin. In all the other Arabian peninsular *Garra* species and in all other *Garra* species investigated the neural spines are shorter in this region, but of the same general configuration and angle as the other neural spines (Fig. 9). In *Garra dunsirei* (Fig. 4) the neural spines are bent sharply back and come to lie almost in parallel with the axis of the centrum.

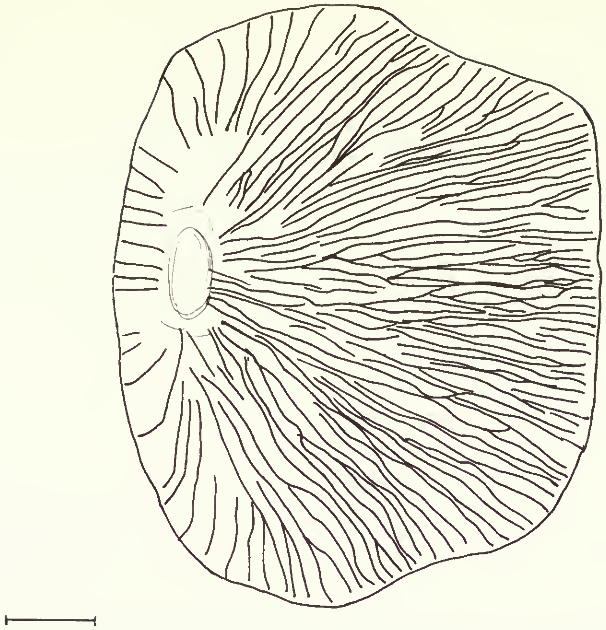

Fig. 3. A scale from the row above the lateral line of the holotype of *Garra dunsirei*. Scale = 0·5 mm.

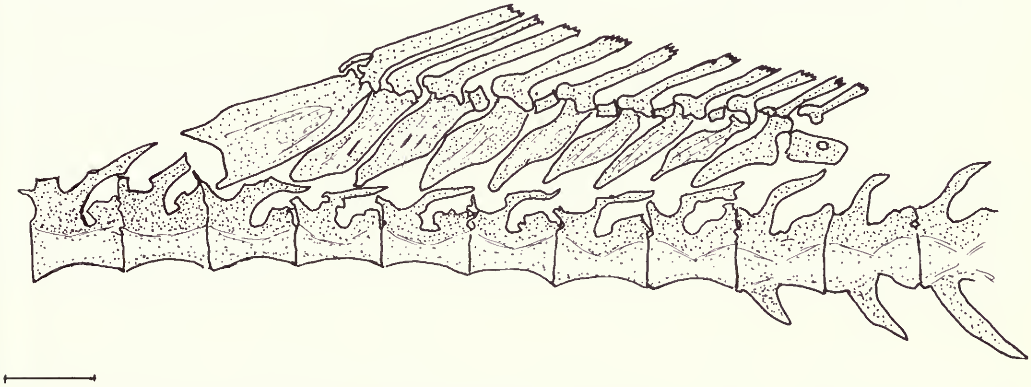

Fig. 4. *Garra dunsirei*. The vertebral column below the dorsal fin to show the unusual profile of the neural spines. For clarity the ribs are omitted. Scale = 1 mm.

Fins. The dorsal fin has only 3(f6) unbranched and 7(f5) or 8(f1) branched rays. The foremost unbranched ray is minute and only visible in a radiograph or an alizarin preparation. The anal fin has 3 unbranched and 5 branched rays (f6). The first unbranched ray is again minute and not visible externally.

Gill rakers. The gill rakers are small in size and few in number. There are 6(f2) or 7(f2) on the lower limb of the first gill arch. They could not be counted in the two smallest specimens.

Pharyngeal bones and teeth. The pharyngeal teeth number 2.4.5–5.4.2 (Fig. 5). The five posterior teeth of the innermost row are thin and have hooked crowns, quite unlike those typical of other *Garra* species from the Arabian peninsula (see Krupp, 1983: figs 23, 27, 40).

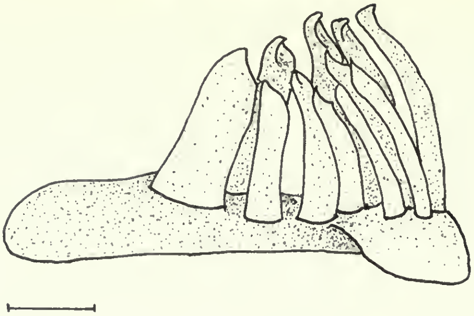

Fig. 5. Left pharyngeal bone of *Garra dunsirei*. Scale = 1 mm.

Coloration. Alcohol preserved specimens are uniform pale, yellowish grey. The ventral surface is only slightly paler than the rest of the body. There are traces of dark pigment near the anterior edge of the pectoral fins, on the dorsal edge of the dorsal fin membrane as well as near the base of the dorsal fin (the last being the typical *Garra* markings). Other fins are colourless.

Living fishes are a dirty white, slightly more heavily dusted with dark pigment dorsally. The cheeks and operculum reflect greenish-gold. The post-opercular spot is inconspicuous but the red of the blood in the gills is clearly visible through the adjacent notch.

Etymology. This species is named in honour of the collector, Mr Andy Dunsire, who has encouraged so many people to search for subterranean fishes, as well as collecting such fish himself in isolated and hazardous regions.

Notes on living specimens. The fishes swim slowly, but continually, usually in a slightly head down position. When resting, they are indifferent to their orientation provided that their ventral surface is in contact with a solid object. They stay near the bottom of the aquarium, very rarely approaching the surface even to take food.

In these aspects they contrast markedly with the blind, hypogean population of *Garra barreimiae* which swims rapidly and swarms at the surface on the introduction of food (Banister, 1984).

Garra dunsirei shows no preference for either light or dark conditions, although a strong light beam shone on an individual will cause it to jerk away after one or two seconds. After that, however, the fishes will come and investigate a localised illuminated patch on the substrate.

Distribution and relationships. Of particular interest is the geographical isolation of *Garra dunsirei* from its congeners. In fact, no primary freshwater fishes have been recorded from this area of Dhofar, the closest natural populations being nearly 400 miles away at Tarim in the Wadi Hadramut to the west and also some 450 miles to the northeast in the Omani Jabal Akhdar. The drainage of this part of the peninsular coast is a series of isolated wadis carrying the run-off due south from the Jabal Qara range to the Arabian sea. On the north side of the Jabal Qara is an interlinked series of wadis that in wetter times would have carried water northwards into the extensive lake or lake system that occupied the site of the Rub al Khali. Krupp (1983) points out that the Jabal Qara range is part of an ancient feature whose presence caused the formation of the internal drainages. Although the internal basin would have permitted fish dispersal northward from Jabal Qara, whether or not it allows fishes from the north access to the streams south of Jabal Qara is unknown. It might be possible to determine the hydrological affinities of this isolated water source were the phylogenetic relationships of *Garra dunsirei* known. For the moment, therefore, neither the hydrological affinities of the sink hole nor the phylogenetic relationships of *Garra dunsirei* can be determined.

Diagnosis. This species can be characterised by the late development of the papillar beds on the mental disc, the papillar bed being only just differentiated at 50 mm SL; also the small eye diameter ($\bar{x}$ = 3·3) and the highly unusual shape of the neural spines below the dorsal fin (see Fig. 4 and p. 62).

Garra lautior sp. nov.

The recognition of this species stems from Krupp (1983: 615) who described six specimens from the Wadi Hadramut as '*Garra*: incertae sedis (1)' but was reluctant to base a species on such a small sample. A search through the collections of the British Museum (Natural History) revealed 13 more specimens.

Holotype. BMNH 1976.4.7: 398, 74 mm SL from the Qasam area, Wadi Hadramut, Yemen, coll. King-Webster.

Paratypes. BMNH 1976.4.7: 399–404, 64–74 mm SL (other details as above); 1976.4.7: 647–648, 71 & 75 mm SL (other detals as above); 1976.4.7: 377–378, 61 & 74 mm SL: (other details as above); 1976.4.7: 645, 80 mm SL from Al-Ghurf, Wadi Hadramut, coll. King-Webster; BMNH 1976.4.7: 366 79 mm SL, from Gheil Umar, Wadi Hadramut, coll. King-Webster.

Description. The description is based on the holotype as 12 paratypes (61–80 mm SL). The measurements are expressed as a percentage of the standard length those of the holotype are included in the range also also given separately in parentheses.

Morphometric data. Body depth $\bar{x}$=22·3, range=20·2–25·0 (22·3) (n=8); head length $\bar{x}$=22·4, range=21·6–23·4 (21·6); eye diameter $\bar{x}$=4·8, range=4·0–5·4 (5·4); mouth width $\bar{x}$=5·7, range=4·4–6·6 (6·1); pectoral fin length $\bar{x}$=19·4, range=18·7–21·5 (19·3); caudal peduncle length $\bar{x}$=17·1, range=15·2–20·0 (15·9); caudal peduncle depth $\bar{x}$=8·6, range=7·7–9·4 (9·3); anterior barbel length $\bar{x}$=2·6, range=1·3–3·2 (3·0); posterior barbel length $\bar{x}$=2·0, range=1·5–3·7 (1·9); dorsal fin height $\bar{x}$=24·8, range=22·9–28·1 (25·5); mental disc maximum length $\bar{x}$=5·4, range=4·7–6·3 (5·5); mental disc maximum width $\bar{x}$=7·0, range=5·7–7·7 (7·3); distance between snout and anus $\bar{x}$=71·4, range=66·6–75·0 (70·2); distance between snout and anal fin origin $\bar{x}$=74·3, range=69·3–77·0 (72·2); distance between snout and pelvic fin origin $\bar{x}$=50·6, range=47·9–52·6 (50·4); distance between snout and dorsal fin origin $\bar{x}$=45·2, range=43·2–46·8 (43·5).

The body has a characteristic, streamlined shape (Fig. 6 and Krupp, 1983: fig. 30). From the pointed snout, the dorsal profile rises smoothly to the insertion of the dorsal fin. Behind the dorsal fin, the trunk diminishes in depth, terminating in a slender caudal peduncle almost exactly half as deep as long. In five specimens the abdomen had collapsed, so a reliable body depth measurement could not be taken. In ventral view, the upper lip is thick and has many small papillae. The shape of

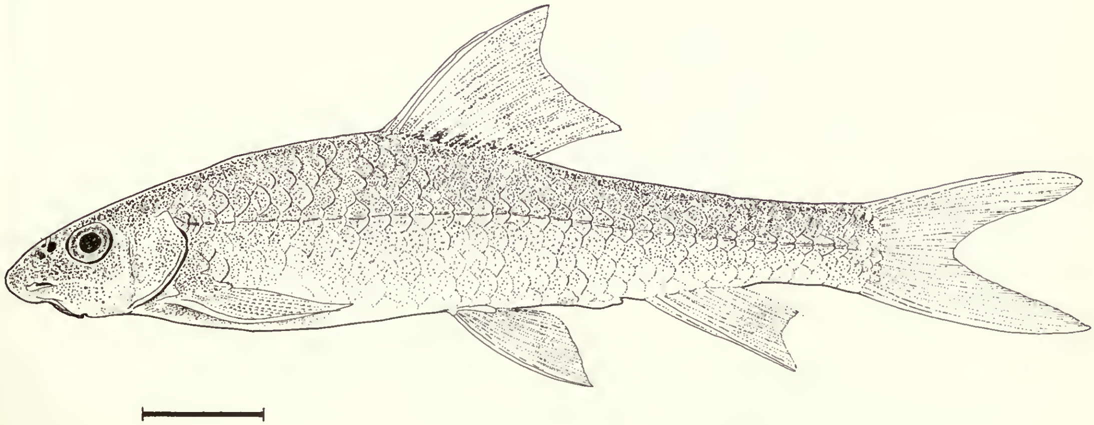

Fig. 6. *Garra lautior*. Holotype. Scale = 10 mm.

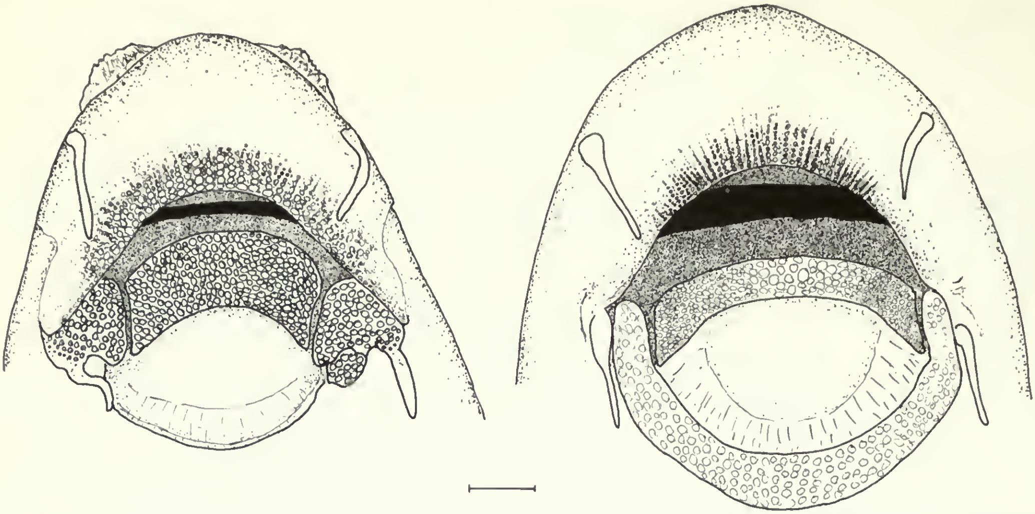

Fig. 7. Details of the distribution of papillae on the frenum, lips and disc of (left) a paratype of *Garra mamshuqua* (74 mm SL ex 1976.4.7: 381–387), and (right) a paratype of *Garra lautior* (74 mm SL ex 1976. 4.7: 399–404) Scale = 0·1 mm.

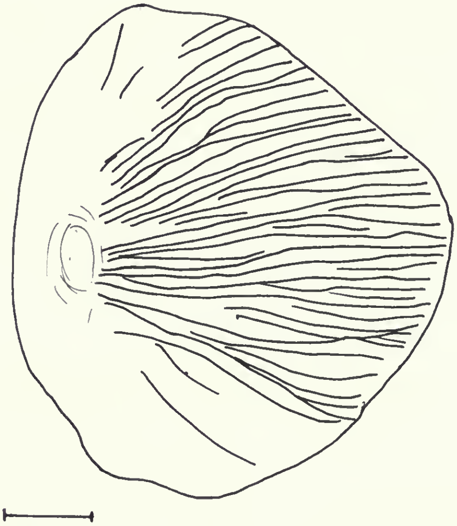

Fig. 8. A scale from the row above the lateral line of *Garra lautior*. Scale = 0·5 mm.

the disc and the disposition of the papillar beds are shown in Figs 2 & 7B. None of the specimens has any tubercles on the head although both mature males and females are present in the sample (see below).

The small size range of the specimens available was insufficient to establish any marked instances of allometric growth.

SQUAMATION. The scales are well developed and slightly lobate. A scale and its striations are shown in Fig. 8. Only two poorly defined growth rings were discernible. In the lateral line series there are 32(f3), 33(f4), 34(f4) or 35(f2) scales. From the dorsal mid-line to the lateral line there are $3\frac{1}{2}$(f9) or $4\frac{1}{2}$(f3) scales and from the lateral line to the pelvic fin base $3\frac{1}{2}$(f13) scales. In front of the anal fin the ventral surface is scaleless. There are 12(f13) scale rows around the least circumference of the caudal peduncle.

VERTEBRAE. In the nine specimens radiographed there are 27(f2), 28(f3), 29(f3) or 30(f1) vertebrae, excluding those comprising the Weberian mechanism. The abdominal vertebrae number 12(f3) or 13(f6) (allowing for the difficulty in identifying the first caudal vertebra). The neural spines below the dorsal fin pterygiophores display the normal alignment and reduction in size of most *Garra* spp (Fig. 9) in contrast to the unique condition in *Garra dunsirei* (Fig. 4).

In all the other species of *Garra* radiographed: viz *G. mamshuqua* Krupp, 1983, *G. barreimiae* Fowler & Steinitz, 1956, *G. sahilia* Krupp, 1983, *G. tibanica* Trewavas, 1941, and *G. dunsirei*, there are 4 interhaemal spine spaces corresponding to the anal fin pterygiophores (Fig. 10), but in *G. lautior* only three interhaemal spine spaces do so correspond (Fig. 11). No particular significance is attached to variations in the shape of the last anal fin pterygiophore. There are 14(f7) or 15(f2) pairs of ribs.

GILL RAKERS. The gill rakers are small, hooked and number 11(f1), 12(f1), 13(f3), 14(f1), 15(f3), 16(f1) and 17(f1) on the lower limb of the first gill arch.

PHARYNGEAL BONES AND TEETH. The pharyngeal teeth number 2.4.5–5.4.2 (Fig. 12). The crowns have shallow spoon-edged depressions, the depression being most sharply edged in newly replaced teeth.

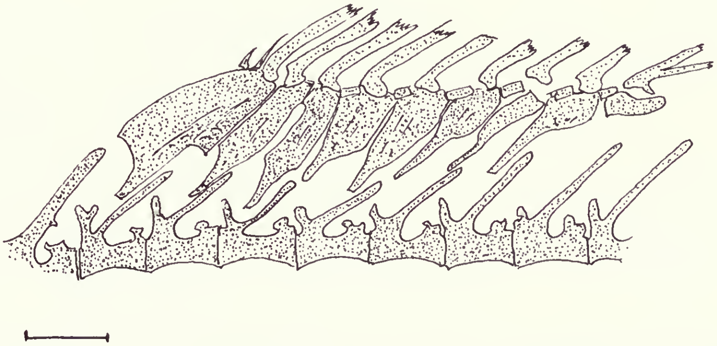

Fig. 9. The vertebral column below the dorsal fin of *Garra lautior* to show the shape of the neural spines. Scale = 1 mm.

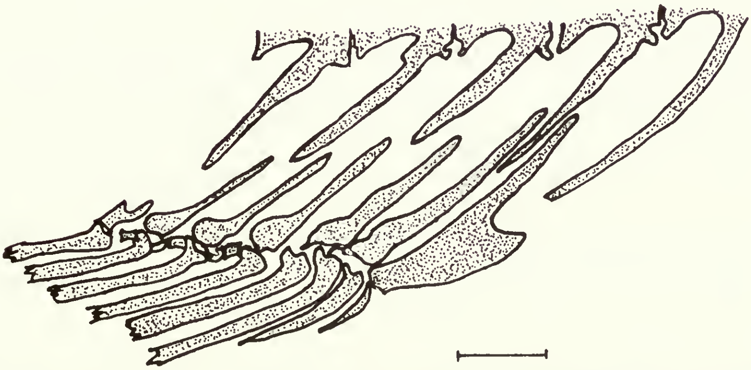

Fig. 10. The anal fin pterygiophores of an unregistered BMNH specimen of *Garra mamshuqua*, 54 mm SL, to show their opposition to four interhaemal spaces. Scale = 1 mm.

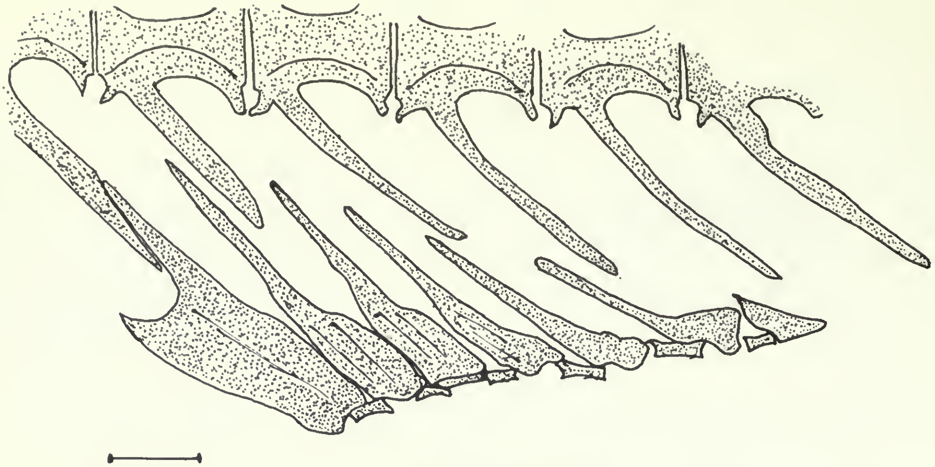

Fig. 11. The anal fin pterygiophores of a specimen of *Garra lautior* (unregistered) to show their opposition to only three interhaemal spaces. Scale = 1 mm.

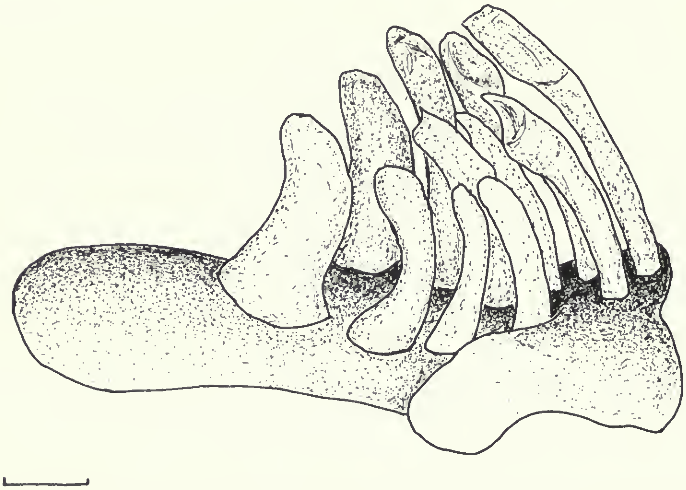

Fig. 12. Left pharyngeal bone of the holotype of *Garra lautior*. Scale = 0·5 mm.

COLORATION. Alcohol preserved specimens are a uniform sandy brown, darker dorsally. The post-opercular spot is a deeper brown, but the *'Garra'* marks at the base of the dorsal fin membrane are not especially conspicuous. The fin membranes are clear.

DISTRIBUTION. This species is known only from localities within the Wadi Hadramut drainage, Yemen.

ETYMOLOGY. The trivial name is the comparative of *lautus*, the Latin for smart or neat and alludes to the neat, streamlined appearance of the fish.

DIAGNOSIS. *Garra lautior* is sympatric only with *Garra mamshuqua* (see below). Although the two species are somewhat similar in body shape, *Garra mamshuqua* can be distinguished by the presence of tubercles on the snout, the very conspicuous *'Garra'* marks on the dorsal fin and behind the operculum and the different disc shape (Fig. 2b & 7b). Very small specimens can be most easily separated on the greater intensity of the post-opercular spot in *Garra mamshuqua*.

Tubercles. Tubercles on the snout are often called nuptial or breeding tubercles (e.g. Wiley & Collette, 1970) or multicellular horny tubercles (Roberts, 1982). The latter author points out that they may occur in both sexes as well as being present before the onset of sexual maturity in *Labeo* species and the homalopterids. In *Garra mamshuqua,* the tubercles are present in both males and females at all stages of sexual maturity and first appear in specimens of 27 mm SL (e.g. in BMNH 1967.4.7: 407–418). It seems probable therefore that in *Garra mamshuqua* the tubercles do not have a solely sexual or reproductive function.

A hydrodynamic function was suggested by Reid (1978) for their occurrence in *Labeo,* since fishes from faster flowing waters had more and larger tubercles than those from quiet waters. The localities where the smooth *Garra lautior* and the tuberculate *Garra mamshuqua* are sympatric were described by the collector (original letter in the BMNH Fish Section archives) as 'a clear stream with stony shallows and deep holes' (Gheil Umar), and also an 'isolated muddy pot-hole below a dam' (Al-Ghurf). Such scanty and seemingly inconsistent information adds nothing to Reid's hydrodynamic hypothesis.

Although the function of the tubercles is not known, it does seem in this case that their presence can be used as a sound diagnostic character to distinguish these two sympatric species. However, it is not suggested that the presence or absence of tubercles is diagnostic for other species.

Discussion

Krupp (1983) also recorded both *Garra tibanica* and *Garra sahilia* from the Wadi Hadramut. *Garra tibanica* was included as a member of the Hadramut fauna solely on specimens collected by Scortecci at Bir el Manzil (14°32′N, 48°51′E *fide* Krupp). Scortecci's Bir el Manzil is shown on the map in Balletto & Spano (1977), which is concerned with the Scortecci expedition and is approximately 14°30′N, 44°30′E or well to the west of the Hadramut.

The Wadi Hadramut record of *Garra sahilia* was based on four fishes, two from Sayun (BMNH 1980.4.24: 8,9) and two from nearby Shibam (BMNH 1980.4.24: 6,7). The latter specimens were identified by Krupp but not listed in his 1983 paper. The four fishes do not correspond to the description, especially in having much longer barbels and the anus closer to the anal fin than in *Garra sahilia.* However, their poor condition precludes confirmation of Krupp's specific determination.

There are some difficulties in establishing which specimens of *Garra sahilia* are types. Krupp (1983: 601) lists 63 specimen (BMNH 1976.4.7: 419, 420–425; 1951. 5.9: 12–65 and 1944.4.3: 1–10) as paratypes but used only 25 specimens in his description. Presumably, the 63 listed paratypes included the 24 actually described (although the largest specimen in his sample, 100·5 mm SL BMNH 1940.2.15: 12–18 was used in the description but not designated a paratype).

Although twice as many *Garra lautior* specimens were available to me than to Krupp, in most respects our descriptions are similar. However, there is substantial discrepancy in our scale counts around the caudal peduncle. In the 13 specimens used here (6 of which were those used by Krupp) I could count only 12 scales, whereas Krupp gives 14(f1) or 16(f5). A similar discrepancy occurs with the same count in *Garra buettikeri* Krupp, 1983, Krupp giving 18(f2) or 20(f18) as the diagnostically high circumpeduncular scale count, whereas in the six BMNH specimens he used in his description I count only 16(f2) or 18(f4) scales. In Krupp's fig. 21 twenty scales would be too many, unless the squamation in the specimen illustrated was unusually asymmetrical. Although Krupp did not indicate how he made his counts I can imagine only one way of counting the number of scale rows around the least circumference of the caudal peduncle. It seems unwise, therefore, to attribute diagnostic significance to this particular meristic feature. No attempt is made in this paper to produce a key to the *Garra* species of the Arabian peninsula. Even a cursory glance at the means and ranges of any particular morphometric or meristic feature used here, in Krupp (1983), in Banister & Clarke (1977) and in many other papers shows that the similarity of means and the extensive overlaps in range usually precludes the use of such characters in a key. Even if the eight peninsular species were initially subdivided by drainage regions (giving groups of 3, 2, 2 and 1) a key based on morphometric and meristic characters would not infallibly separate the sympatric species. The major diagnostic features are regrettably very difficult to quantify. At the moment the most useful characters are the overall body shape, the shape of the mental disc and the distribution of papillae thereon, and the colour pattern. Although details of the mental disc serve to distinguish species, based on the samples available, the variation in at least one species, *Garra tibanica* (Balletto & Spano, 1977: fig. 6) makes one wonder whether it will remain useful when more populations are discovered.

Krupp 1983: 603–615 provided a useful list of all the specimens he examined. There are, however, some confusions in the BMNH register numbers in his list and these and some other errors are corrected below.

Garra sahilia sahilia (p. 603)
Sample No. 10 for Wadi Abd read Wadi Anad 44°50′E, 13°17′N
No. 14 for 1976.4.7: 443–460 read 1976.4.7: 460
No. 15 for 1910.1.28: 1–3 read 1870.1.28: 1–3

Garra sahilia gharbia (p. 604)
Sample No. 5 for 1976.4.7: 646–354 read 1976.4.7: 346–349

Garra tibanica tibanica (p. 608)
Sample No. 5 for 1976.4.7: 443–460 read 1976.4.7: 443–459
No. 11 for 1952.5.7: 13–18 read 1952.5.7: 13–17
No. 17 for 1976.4.7: 346–356 read 1976.4.7: 350–354

Garra incertae sedis (p. 615)
Sample No. 1 for 1976.4.7: 374–377 read 1976.4.7: 377
No. 3 for 1976.4.7: 380–406 read 1976.4.7: 380–396

Acknowledgements

I particularly wish to thank the collectors for their enthusiasm in seeking for fish life in such an inhospitable environment. Without the efforts of such people, our knowledge of fish distribution and habitats would increase more slowly. My colleagues, Dr P. J. P. Whitehead and Mr A. C. Wheeler offered constructive comments on the manuscript. My thanks go to them and to Gordon Howes for illustrating the new species and to Joan Ellis for typing the paper.

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British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl, with a section on the biogeographic context by Malcolm Coe.

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as on conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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Bulletin of the British Museum (Natural History)

A revision of the Suctoria (Ciliophora, Kinetofragminophora) 5. The *Paracineta* and Corynophrya problem

Colin R. Curds

Zoology series Vol 52 No 2 27 February 1987

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A revision of the Suctoria (Ciliophora, Kinetofragminophora) 5. The *Paracineta* and *Corynophrya* problem

Colin R. Curds
Zoology Department, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

The continual drift in the diagnosis of the unrelated genera *Paracineta* and *Corynophrya* causes considerable taxonomic problems and confusion at several levels in classification. The transfer of *Paracineta crenata* and *Paracineta homari* into the genus *Actinocyathula* has allowed the present review to be based, as far as possible, on the original diagnoses of the genera. In addition to those mentioned above, the species of four other genera, *Pelagacineta, Loricophrya, Anthacineta* and *Flectacineta* are reviewed since some have been previously associated in some way with the *Paracineta–Corynophrya* problem in the past.

A new diagnosis for each genus is given with a key to its constituent species and where appropriate a genotype has been designated to encourage taxonomic stability. All species are described and figured.

Introduction

There is still considerable confusion and disagreement on the generic diagnoses of *Paracineta* Collin, 1911 and *Corynophrya* Kahl, 1934. The purpose of this publication is to review the species involved, to amend previous diagnoses and to assign type species to the genera in an attempt to establish taxonomic stability. The genus *Paracineta* was erected in order to take account of those loricate suctoria with an apical group of tentacles that reproduced by external budding and that were longitudinally symmetrical. In his original generic description, Collin (1911) included the three species *Paracineta crenata* (Fraipont, 1878), *P. homari* (Sand, 1899) and *P. patula* (Claparède & Lachmann, 1861) but failed to designate the type species. In his later taxonomic revision, Collin (1912) transferred several more species into the genus including *Paracineta limbata* (Maupas, 1881), *P. vorticelloides* (Fraipont, 1878), *P. jorisi* (Sand, 1895), *P. parva* (Sand, 1899), *P. multitentaculata* (Sand, 1895), *P. livadiana* (Mereschkowsky, 1881), *P. elegans* (Imhoff, 1883) and *P. bifaria* (Stokes, 1887). Collin (1911, 1912) stressed that although external budding was a prime feature of the genus both *Paracineta crenata* and *P. homari* in fact reproduced by semi-external budding (the semi-invaginative budding of Batisse, 1975). At the time this method was thought to be only a slight variation on the external budding theme and of little significance.

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Modern workers however consider the different modes of budding to be of great taxonomic importance and that there is a distinct difference between semi-invaginative and external budding. Nevertheless, the two species remained in their original genus until Batisse (1975) suggested their transfer into the genus *Corynophrya* Kahl, 1934 which had been originally erected for a heterogenous assemblage of aloricate suctoria reproducing by internal budding. Although the suggestion by Batisse (1975) may appear strange, since the two species in question are loricate and reproduce differently, it should be pointed out that the generic diagnosis of *Corynophrya* has drifted considerably since that originally outlined by Kahl (1934). However, Batisse (1975) had not taken into account that *Paracineta crenata* can be regarded to be congeneric with *Actinocyathus cidaris* Kent, 1882 and would be more neatly transferred into the latter older genus. Jankowski (1981) is also apparently of a similar opinion since he suggested that the name *Actinocyathus* might replace that of *Paracineta*. The name *Actinocyathus* was shown by Corliss (1960) to be preoccupied and he suggested the replacement name *Actinocyathula* Corliss, 1960.

Kahl (1934) erected the genus *Corynophrya* to include the mostly marine assemblage of suctoria which Collin (1912) had gathered together in his third group within the genus *Discophrya*. The major diagnostic features were that they reproduced by internal budding, did not possess a lorica, were rounded in cross-section, had one type of tentacle that was restricted to the apical surface and had a rounded, compact nucleus. According to Kahl (1934) the following species held these features in common, *Corynophrya marina* (Andrusov, 1886), *C. conipes* (Mereschkowsky, 1879), *C. macropus* (Meunier, 1910), *C. lyngbyi* (Ehrenberg, 1833), *C. francottei* (Sand, 1895), *C. campanula* (Schröder, 1907), *C. interrupta* (Shröder, 1907) and *C. stueri* (Schröder, 1911). Kahl agreed with Collin (1912) and placed the genus in the family Discophryidae where it remained until Batisse (1975) transferred it into the Thecacinetidae. More recently Jankowski (1978) has transferred three of the species, which clearly have elongate to branched macronuclei and multiple endogenous buds, into the new genus *Pelagacineta* Jankowski, 1978.

Genus *ACTINOCYATHULA* Corliss, 1960

Actinocyathus Kent, 1882
Corynophrya sensu Batisse, 1975
Paracineta sensu Jankowski, 1978
Faltacineta Jankowski, 1982

The genus *Actinocyathus* was erected by Kent (1882) for those resembling *Ephelota* in general form but borne upon a stalked lorica. Kent's (1882) diagnosis also stated that the tentacles were retractile but not capitate. However, Kent further stated in his description of the type species *Actinocyathus cidaris* Kent, 1882 that he only saw the tentacles in the contracted state which leaves the absence of capitate tentacles open to considerable doubt. There seems to be little doubt that the organism depicted by Dons (1922) which he calls *Paracineta crenata* (Fraipont) forma *pachyteca* Collin (Dons mispelling of *pachytheca*) is congeneric with *Actinocyathus* and conspecific with *Acineta crenata* Fraipont, 1878. In view of this the two species *Paracineta crenata* (Fraipont, 1878) and *P. homari* (Sand, 1899) which both reproduce by semi-invaginative budding are transferred to *Actinocyathula* Corliss, 1960. Jankowski (1982) erected the genus *Faltacineta* Jankowski, 1982 for the two marine epizoic species *Paracineta pleuromammae* Steuer, 1928 and *Paracineta gaetani* Sewell, 1951. However, the former species *P. pleuromammae* is clearly depicted showing semi-invaginative budding and for this reason the two are transferred to *Actinocyathula* for the first time.

Diagnosis of *Actinocyathula*

Marine suctorians whose ovoid-shaped body is restricted to the anterior half of the lorica. Lorica cup-shaped, never laterally compressed, borne upon a stalk and attached to marine invertebrates such as crustacea, hydroid colonies and calcareous sponges. Tentacles in a single group that is restricted to the apical region of the body. Actinophores absent. Reproduction by semi-invaginative budding.

Key to the species of *Actinocyathula*

1	Stalk equal to or less than lorica length, epizoic on crustacea	3
	Stalk greater than lorica length, epizoic on invertebrates other than crustacea	2
2	Lorica smooth	***A. cidaris***
	Lorica striated transversely	***A. crenata***
3	Posterior region of lorica broadly rounded	***A. homari***
	Posterior of lorica distinctly narrow	4
4	Lorica elongate, stalk usually less than half lorica length	***A. pleuromammae***
	Lorica width and stalk length approximately equal to lorica length	***A. gaetani***

Species descriptions

Actinocyathula cidaris Corliss, 1960

Actinocyathus cidaris Kent, 1882

Description (Fig. 1). This the type species is a small (40 µm long), marine, loricate suctorian. The ovoid body has a flattened base and protrudes from the apical region of the lorica. Tentacles retractile, radiating from the anterior surface of body. Lorica surface smooth, triangular in outline, rounded in cross-section. Apical edge of lorica bends inwards to form a thin cup-like platform in which the zooid is located. Lorica mounted on slender but rigid stalk that is 3–4 times the lorica length. Epizooic on the calcareous sponge *Grantia compressa*. Contractile vacuole may be single or double. Nuclear and reproductive features not described.

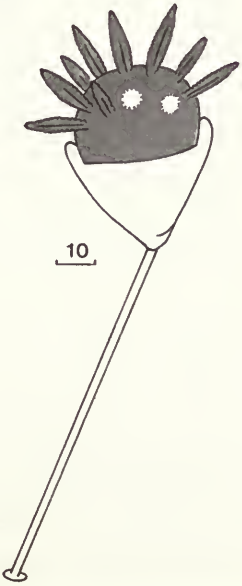

Fig. 1 *Actinocyathula cidaris* after Kent, 1882 (called *Actinocyathus cidaris*).

Actinocyathula crenata n. comb.

Acineta crenata Fraipont, 1878
Acineta saifulae Mereschkowsky, 1877
Paracineta crenata Collin, 1911
Paracineta crenata var. *pachytheca* Collin, 1912
Paracineta crenata forma *pachyteca* Dons, 1922
Corynophrya crenata Batisse, 1975
Miracineta saifulae Jankowski, 1981

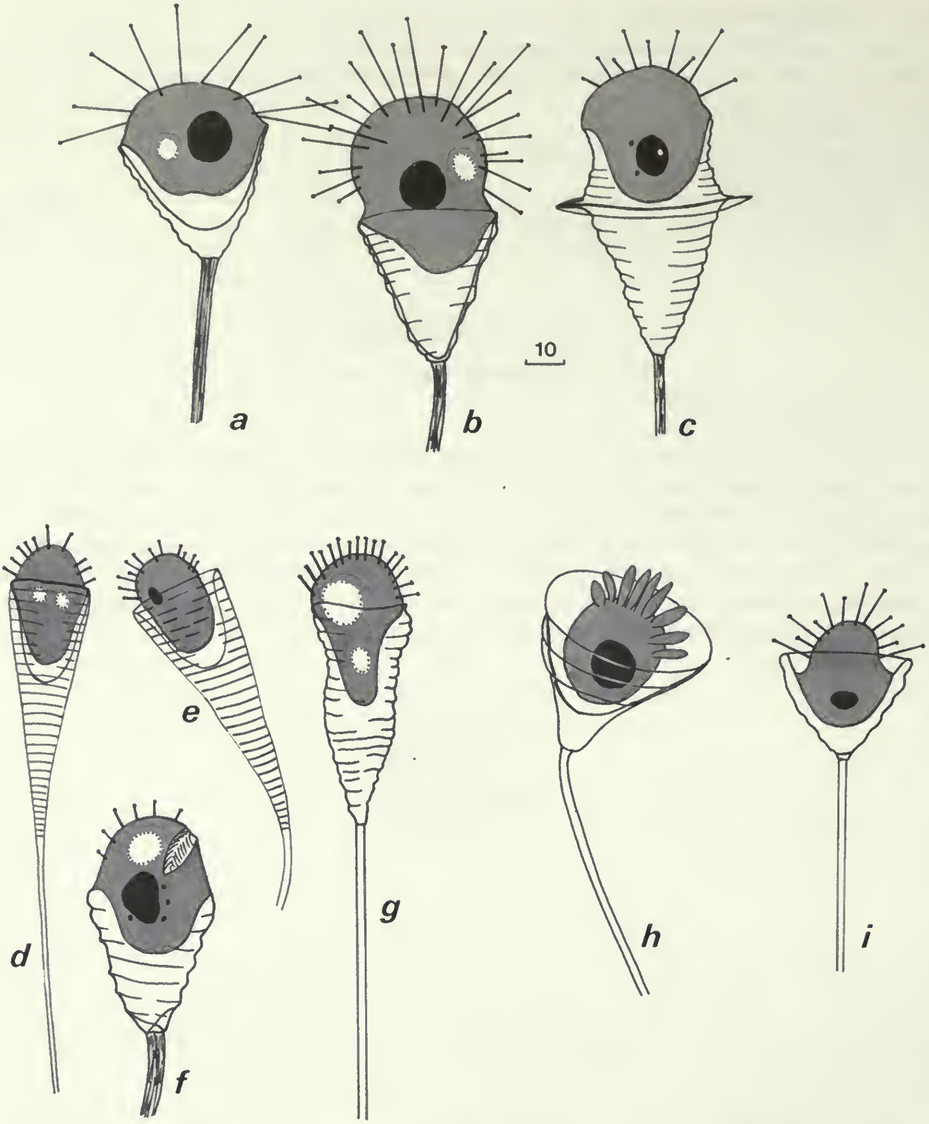

Fig. 2 *Actinocyathula crenata*: (a–c) after Collin, 1912 (called *Paracineta crenata*); (d,e) after Mereschkowsky, 1877 (called *Acineta saifulae*); (f) after Collin, 1912 (called *Paracineta crenata*); (g) after Fraipont, 1878 (called *Acineta crenata*); (h) after Dons, 1922 (called *Paracineta crenata* var. *pachytheca*); (i) after Wailes, 1928 (called *Paracineta crenata* var. *pachytheca*).

DESCRIPTION (Fig. 2). Medium (75 µm long), marine, loricate suctorian. The ovoid body protrudes from the apical region of the lorica. Capitate tentacles sometimes retractile, radiating from the anterior surface of body. Lorica surface crenulated with three to many transverse striations, triangular to elongate in outline, rounded in cross-section. There is a thin cup-like platform in which the zooid is located. Lorica mounted on slender stalk that is 3–4 times the lorica length. Epizooic on a variety of marine invertebrates including the hydroids *Clytia volubilis, Leptoscyphus grigoriewi* and *Perigonimus repens* and the polychaete *Aphrodite aculeata*. Single contractile vacuole located laterally. Spherical macronucleus centrally positioned. Reproduction by semi-invaginative budding. Swarmer not described.

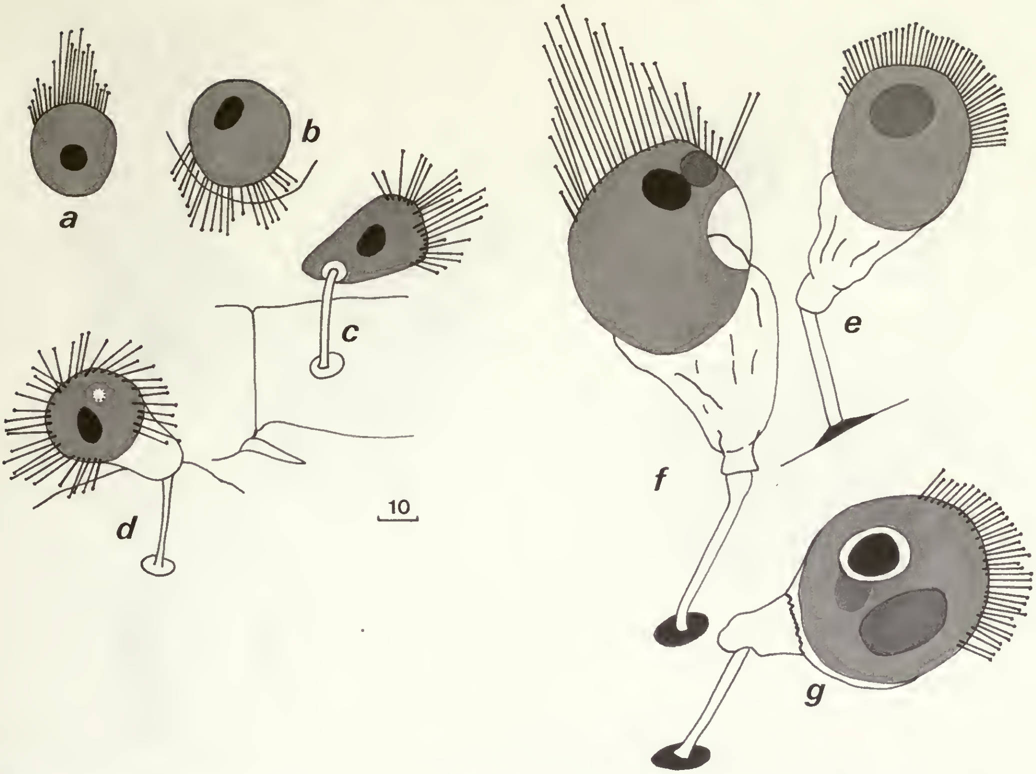

Fig. 3 *Actinocyathula gataeni*: (a–d) various growth stages; (e–g) adults; all after Sewell, 1951 (called *Paracineta gataeni*).

Actinocyathula gataeni (Sewell, 1951) n. comb.

Paracineta gataeni Sewell, 1951
Faltacineta gataeni Jankowski, 1982

Description (Fig. 3). Small (30–55 µm diameter), marine, loricate suctorian. The ovoid body protrudes from the apical region of the lorica. Tentacles radiate out from the anterior body surface. Lorica surface usually smooth but sometimes with transverse wrinkles, triangular in outline, rounded in cross-section. Lorica mounted on a robust rigid stalk that is usually less than the lorica length. Lorica sometimes mounted eccentrically on stalk. Epizooic on the copepods *Gaetanus antarcticus* Wolfendon and *G. curvicornis* Sars. Macronucleus spherical. Reproduction and swarmer not described.

Actinocyathula homari n. comb.

Acineta homari Sand, 1899
Paracineta homari Collin, 1911
Corynophrya homari Batisse, 1975

Description (Fig. 4). Small (25–40 µm long), marine, loricate suctorian. The ovoid body protrudes from the apical region of the lorica. Tentacles retractile, radiating out from the anterior body surface. Lorica surface smooth, triangular to bell-shaped in outline, rounded in cross-section. Lorica mounted on a robust rigid stalk that rarely exceeds the lorica length. Lorica sometimes mounted eccentrically on stalk. Epizooic on a variety of decapod crustacea. Single contractile vacuole located centrally or laterally. Macronucleus spherical, located at posterior of body. Reproduction by semi-invaginative budding. Swarmer not described.

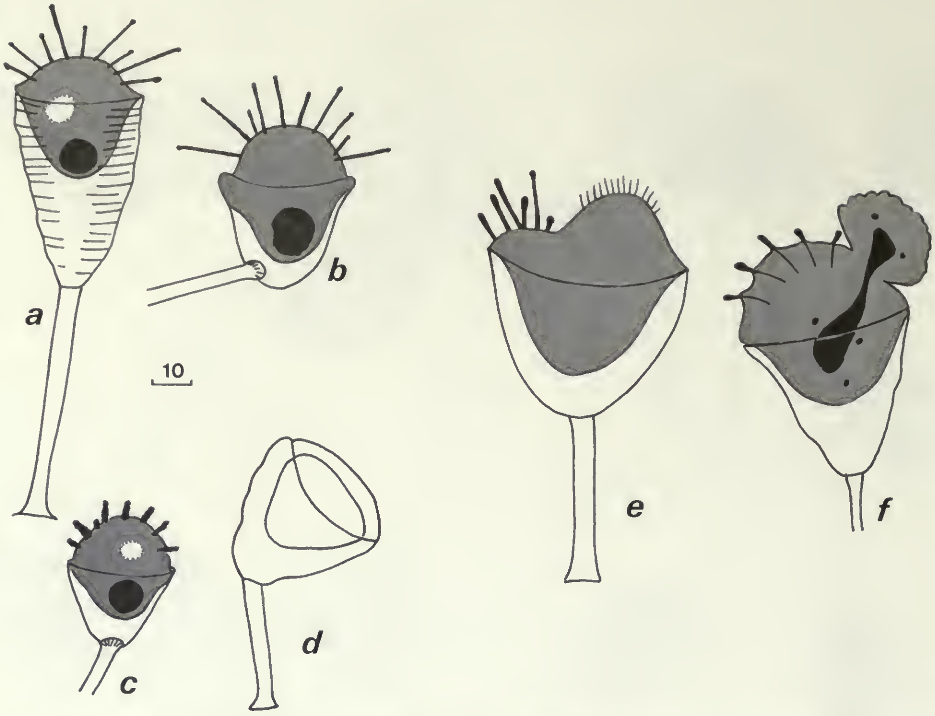

Fig. 4 *Actinocyathula homari*: (a–d) after Collin, 1912 (called *Paracineta homari*); (e,f) after Sand, 1899 (called *Acineta homari*).

Actinocyathula pleuromammae (Steuer, 1928) n. comb.

Paracineta pleuromammae Steuer, 1928
Faltacineta pleuromammae Jankowski, 1982

Description (Fig. 5). Medium (60–115 µm long), marine, loricate suctorian. The ovoid body protrudes from the apical region of the lorica. Tentacles radiate out from the anterior body surface. Lorica surface with irregular transverse striations, elongated cone, rounded in cross-section. Lorica mounted on a robust rigid stalk that is less than half the lorica length. Epizoic on the copepods *Pleuromamma abdominalis* and *P. xiphias*. Single contractile vacuole located laterally. Macronucleus spherical, located centrally. Reproduction by semi-invaginative budding. Swarmer ovoid with many transverse ciliary rows.

Genus ***CORYNOPHRYA*** Kahl, 1934

Pelagacineta Jankowski, 1978 *pro parte*

The genus was orginally erected by Kahl (1934) to include a heterogenous collection of mainly marine species. He stated that the major features distinguishing it from other genera included internal budding, a single apical group of tentacles and a rounded, compact macronucleus. Kahl (1934) included eight species in his genus but three have recently been transferred to the new genus *Pelagacineta* by Jankowski (1978). Kahl (1934) followed the original higher classification system of Collin (1912) and placed the genus in the family Discophryidae where it remained until Batisse (1975) transferred it into the Thecacinetidae which demands reproduction by semi-invaginative budding. The latter step was taken because Batisse (1975) had included *Actinocyathula (Paracineta) crenata* and *A. homari* in the genus. In fact the mode of budding has only been described for one of the five remaining species, where in *Corynophrya lyngbyi* it is endogenous.

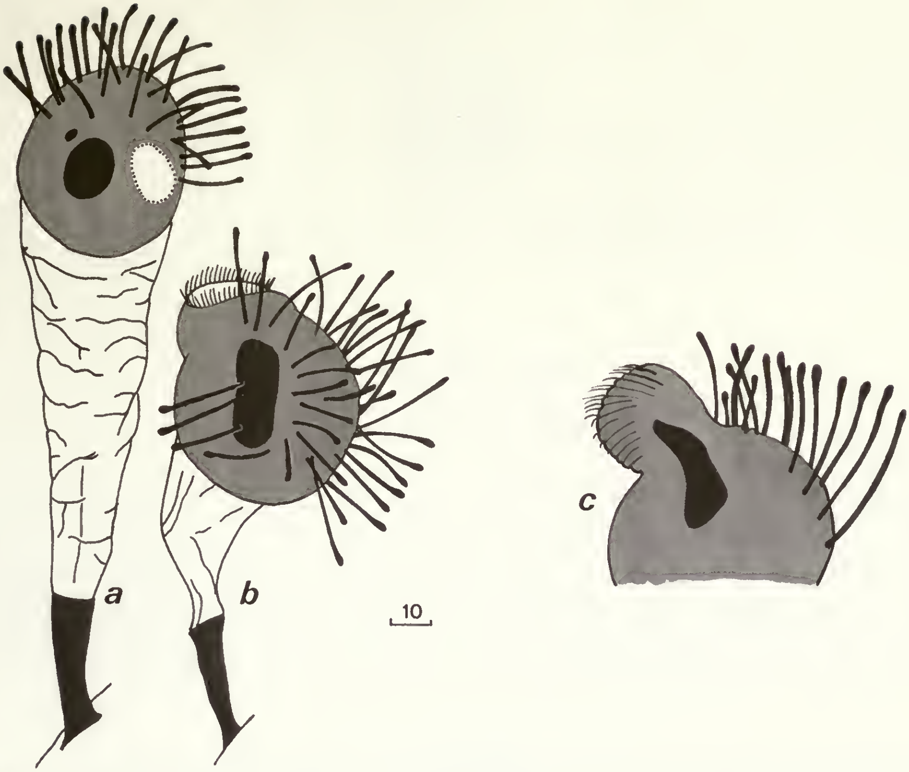

Fig. 5 *Actinocyathula pleuromammae*: (a–c) after Steuer, 1928 (called *Paracineta pleuromammae*).

However, Jankowski (1981) was recently of the opinion that genera in his family Corynophryidae reproduce exogenously although he gave no practical evidence for that conclusion. Of those which Kahl (1934) originally included in the genus only four, *Corynophrya macropus*, *C. conipes*, *C. lyngbyi* and *C. francottei* remain in the present review. The anterior notch in the body of *Corynophrya marina* has been interpreted to indicate invaginative budding and will be transferred to an appropriate genus in a later publication. One other species, *Ephelota columbiae* Wailes, 1943 is included in the genus for the first time since it bears only one type of tentacle whereas there are two types in *Ephelota*. The five species that are included have several features in common, they all have a compact rounded macronucleus, a single apical group of tentacles that are both retractile, prehensile and suctorial and in most there is a conical stalk that clearly narrows towards its base. The species most completely described is *Corynophrya lyngbyi* and this is designated to be the type species in an attempt to establish taxonomic stability.

Diagnosis of *Corynophrya*

Mainly marine, aloricate suctorians whose body shape is spherical to ovoid, rounded in cross section. Borne upon a stalk which is commonly stout near to the zooid narrowing markedly towards its base. Usually epizooic on hydroids, crustacea and polychaetes but also noted on marine algae. Tentacles prehensile and retractile in a single group that is restricted to the apical region on the body. Actinophores absent. Macronucleus usually spherical. Reproduction by endogenous budding.

Key to the species of *Corynophrya*

1 Stalk long, at least 3 times length of body 4
Stalk short, up to twice length of body 2

2	Freshwater, tentacles wide at base, narrowing towards capitate ends	***C. tumida***
	Marine, sides of tentacles parallel, do not narrow towards capitate ends	3
3	Body spherical and regular	***C. columbiae***
	Body ovoid, uneven with folds	***C. symbiotica***
4	Stalk striated transversely	***C. conipes***
	Stalk striated longitudinally or without striations	5
5	Macronucleus spherical	6
	Macronucleus in shape of horseshoe	***C. lyngbyi***
6	Stalk markedly wider near zooid, narrowing towards base	***C. macropus***
	Sides of stalk parallel, stalk does not narrow towards base	***C. francottei***

Species descriptions

Corynophrya lyngbyi (Ehrenberg, 1833) Kahl, 1934

Acineta lyngbyi Ehrenberg, 1833
Podophrya lyngbyei Claparède & Lachmann, 1859 *non* Robin, 1879
Tokophrya lyngbyei Bütschli, 1889
Discophrya lyngbyei Collin, 1912

DESCRIPTION (Fig. 6). This the type species is a small to medium (40–80 µm), marine, aloricate suctorian. The ovoid body is oval in section and slightly wider anteriorly. The retractile, capitate tentacles located on the anterior body surface. Stalk long (120–400 µm), at least four times

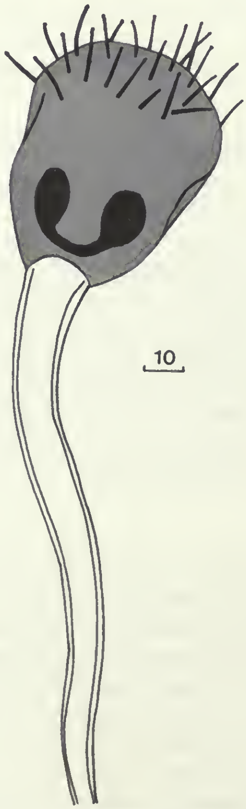

Fig. 6 *Corynophrya lyngbyi* after Fraipont, 1878 (called *Podophrya lyngbyi*).

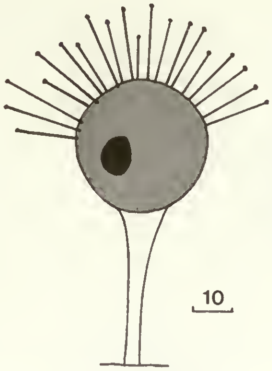

Fig. 7 *Corynophrya columbiae* after Wailes, 1943 (called *Ephelota columbiae*).

the body length. Stalk wider near zooid than at its base. Attached to hydroid colonies such as *Sertularia* and *Clytia* as well as marine algae. There are one or two contractile vacuoles. Macronucleus spherical in the young adult but this elongates into a horse-shoe shape at maturity. Reproduction by endogenous budding which may be multiple. Swarmer not described.

Note. The specific epithet has been consistently mispelt by several authors over many years. Ehrenberg's (1833) original spelling was *lyngbyi* but later (1838) in his atlas the name appears as *lyngbyei* and it was this spelling that was used by several later authorities.

Corynophrya columbiae n. comb.

Ephelota columbiae Wailes, 1943

Description (Fig. 7). This is a small (30–60 µm), marine, aloricate suctorian. The spherical to ovoid body is round in section. The retractile, capitate tentacles located on the anterior half of body surface. Stalk usually short (50–200 µm), and usually less than three times the body length. Stalk wide near zooid narrowing towards the base. Attached to crustacea in large numbers. Macronucleus spherical, centrally located. Reproduction not described.

Corynophrya conipes (Mereschkowsky, 1877) Kahl, 1934

Acineta conipes Mereschkowsky, 1877
Podophrya conipes Mereschkowsky, 1879
Tokophrya conipes Bütschli, 1889

Description (Fig. 8). This is a large (100–190 µm), marine, aloricate suctorian. The ovoid to pyriform body is oval in section and widens anteriorly. The retractile, capitate tentacles located mainly on the anterior body surface. Stalk long (800–1500 µm), usually 8–10 times the body length. Stalk distinctly wider near zooid than at its base, finely striated transversely and usually with two distinct annuli situated about a third of the way down the stalk. Attached to marine algae such as *Ptilota* and *Ceramium*. Single anterior contractile vacuole. Macronucleus spherical, located centrally or subcentrally. Reproduction and swarmer not described.

Corynophrya francottei (Sand, 1895) Kahl, 1934

Tokophrya francottei Sand, 1895
Discophrya francottei Collin, 1912

Description (Fig. 9). This is a small (50–60 µm), marine, aloricate suctorian. The retractile, capitate tentacles are located on the anterior surface of the spheroidal body. Stalk long (100–230 µm), at least three times the body length, retaining a constant diameter along its entire length. Attached to hydroid colonies such as *Sertularia* and *Ceramium*. There is a single

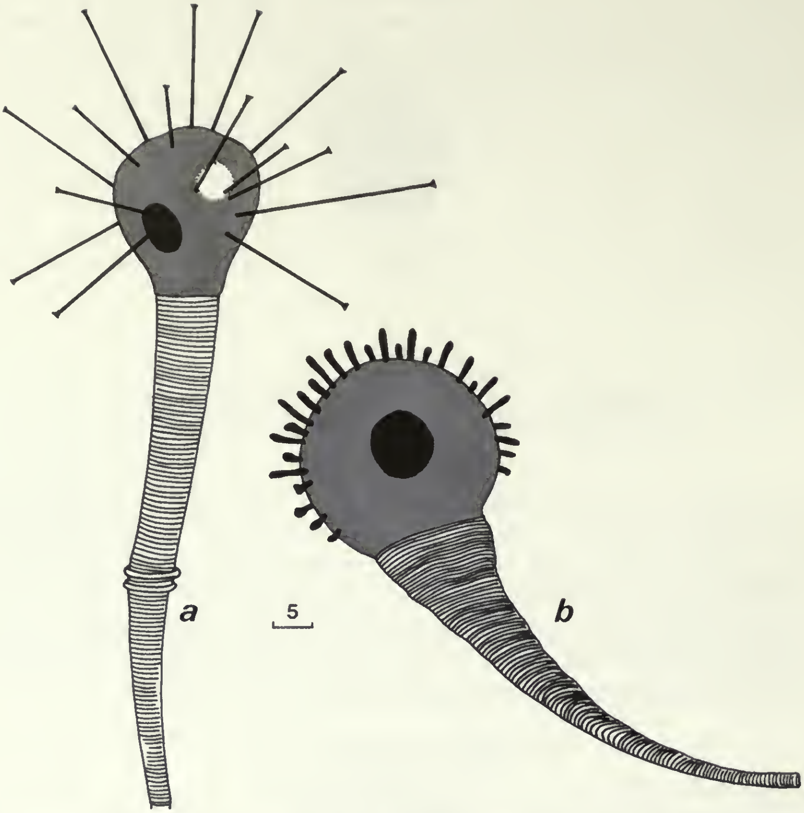

Fig. 8 *Corynophrya conipes*: (a) after Mereschkowsky, 1879 (called *Podophrya conipes*); (b) after Meunier, 1910 (called *Podophrya conipes*).

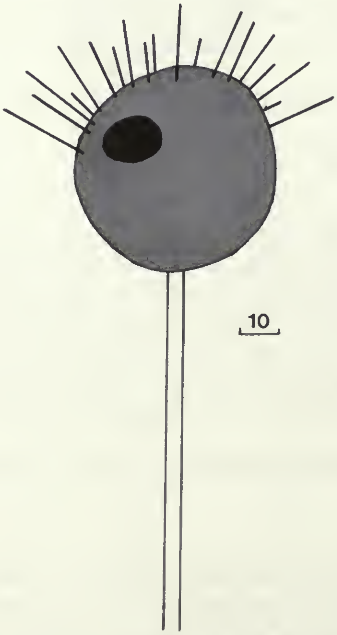

Fig. 9 *Corynophrya francottei* after Sand, 1895 (called *Tokophrya francottei*).

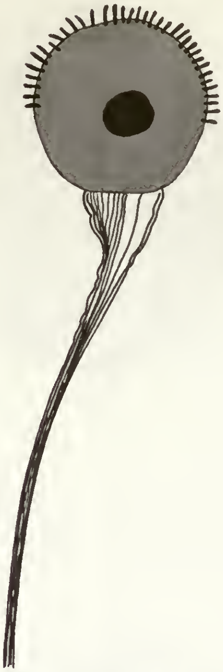

Fig. 10 *Corynophrya macropus* after Meunier, 1910 (called *Podophyra macropus*).

marginal contractile vacuole. Macronucleus oval to spherical, located centrally or subcentrally. Reproduction and swarmers not described.

Corynophrya macropus (Meunier, 1910) Kahl, 1934

Podophrya macropus Meunier, 1910

Description (Fig. 10). This is an incompletely defined species whose size has not been recorded, marine, aloricate. The body is spherical in shape and carries retractile, capitate tentacles on its anterior surface. Stalk long, at least three times the body length. Stalk, which is wider near the zooid than at its base, is distinctly striated, longitudinally along its entire length. Macronucleus spherical, located centrally. Reproduction and swarmer not described.

Corynophrya symbiotica Jankowski, 1981

Description (Fig. 11). This is a medium (80–105 µm), marine, aloricate suctorian. The ovoid body has rather bumpy irregular appearance with some longitudinal folds. The retractile tentacles occupy the entire domed anterior body surface. Stalk comparatively short (up to 90 µm), about same as the body length. Stalk slightly wider near zooid than at its base. Attached to arctic polychaete worms belonging to the family Aphroditidae. There is a single anterior contractile vacuole. Macronucleus spherical, located centrally. Reproduction and swarmer not described.

Corynophrya tumida (Gajewskaja, 1933) Matthes, 1954

Discophrya tumida Gajewskaja, 1933

Description (Fig. 12). This is a small (50 µm), freshwater, aloricate suctorian. The ovoid body is round in section and slightly wider posteriorly. The retractile, capitate tentacles are rather wider at the base and occupy the anterior half of the body surface. Stalk short (60–70 µm), only just longer than the body. Stalk wider near zooid than at its base and distinctly striated transversely at infrequent intervals along its length. The stalk is also irregularly striated longitudinally.

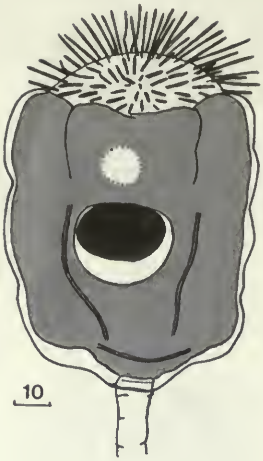

Fig. 11 *Corynophrya symbiotica* after Jankowski, 1981.

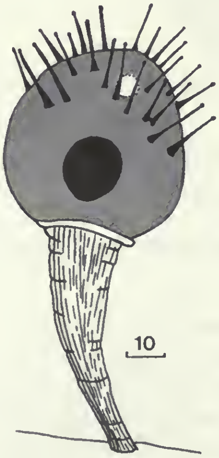

Fig. 12 *Corynophrya tumida* after Gajewskaja, 1933 (called *Discophrya tumida*).

Attached to gammarid crustacea in Lake Baikal. There is a single anterior contractile vacuole. Macronucleus spherical, located centrally. Reproduction and swarmer not described.

Genus ***PELAGACINETA*** Jankowski, 1978

Schröder (1907) first described the two marine species *Tokophrya interrupta* and *T. campanula* which resembled *Ephelota* in some respects and *Podocyathus* in others. They resembled *Ephelota* in their multiple endogenous method of budding but *Ephelota* is without a thecostyle and has two different types of tentacles. Similarly they resembled *Podocyathus* in their overall structure but reproduced differently from that genus. Schröder (1911) later added a further species *T. steueri* to the group but still placed it in *Tokophrya* a genus typified by the absence of a lorica. Collin (1912) was the first to transfer the three species out of *Tokophrya* and he grouped them with several other misfits into his third section of the genus *Discophrya*. Kahl (1934) later erected the new genus *Corynophrya* for Collin's third section where they remained until the genus *Pelagacineta* was defined by Jankowski (1978) for those species 'like *Podocyathus* but with multiple endogenous budding'. Jankowski (1978) designated *P. interrupta* (Schröder, 1907) to be the type species and included *P. campanula* (Schröder, 1907) in the new genus. In the current revision the diagnosis is elaborated for the sake of clarity and some other species are transferred to the genus for the first time.

Diagnosis of *Pelagacineta*

Marine suctoria with lorica-like thecostyle. Body shape ovoid, discoidal or pyriform, rounded in cross section, actinophores absent. Stalk widens anteriorly to form lorica-like thecostyle. Single type of retractile tentacle present, arranged in one or two anterior groups. Attached to copepods or marine algae. Macronucleus typically elongate and often branched. Reproduction by multiple endogenous budding. Swarmers ovoid partially ciliated with several longitudinal kineties.

Key to the species of *Pelagacineta*

1	Tentacles in single anterior group	***P. campanula***
	Tentacles in two anterior groups	2
2	Only 2 tentacles present, attached to algae	***P. dibdalteria***
	Many tentacles present, attached to copepods	3
3	Macronucleus elongate but not branched, body ovoid but not discoidal	***P. euchaetae***
	Macronucleus elongate and branched, body sometimes discoidal	***P. interrupta***

Species descriptions

Pelagacineta interrupta (Schröder, 1907) Jankowski, 1978

Tokophrya interrupta Schröder, 1907
Discophrya interrupta Collin, 1912
Corynophrya interrupta Kahl, 1934

Description (Fig. 13). This the type species is a medium (100–140 µm long), marine suctorian with thecostyle. The ovoid body may be dorso-ventrally compressed and discoidal in shape lying at the top of a thecostyle that widens considerably to form a lorica-like anterior region. Stalk region hollow, 2–3 times the length of the lorica part of the thecostyle, terminating in a longitudinally striated basal disc. Many retractile, capitate tentacles located anteriorly arranged in two fascicles. Attached to marine copepods such as *Euchaeta* and *Metridia* reported from antarctic waters. Shape of macronucleus variable, always elongate and frequently branched. Reproduction by multiple endogenous budding producing oval swarmers partially ciliated with many kinetics on part of the ventral body surface.

Pelagacineta campanula (Schröder, 1907) Jankowski, 1978

Tokophrya campanula Schröder, 1907
Tokophrya steueri Schröder, 1911
Discophrya campanula Collin, 1912
Discophrya steueri Collin, 1912
Corynophrya campanula Kahl, 1934
Corynophrya steueri Kahl, 1934

Description (Fig. 14). This is a medium (100–150 µm long), marine suctorian with thecostyle. The ovoid body may be dorso-ventrally compressed and discoidal in shape lying at the top of a thecostyle that widens considerably to form a cupped lorica-like anterior region. Stalk region hollow, 1–3 times the length of the lorica part of the thecostyle, terminating in a longitudinally striated basal disc. Many retractile, capitate tentacles located anteriorly arranged in a single fascicle sometimes surrounded by an outer ring of short tentacles. Attached to marine copepods such as *Euchaeta* and *Metridia* reported from antarctic waters. Shape of macronucleus variable but

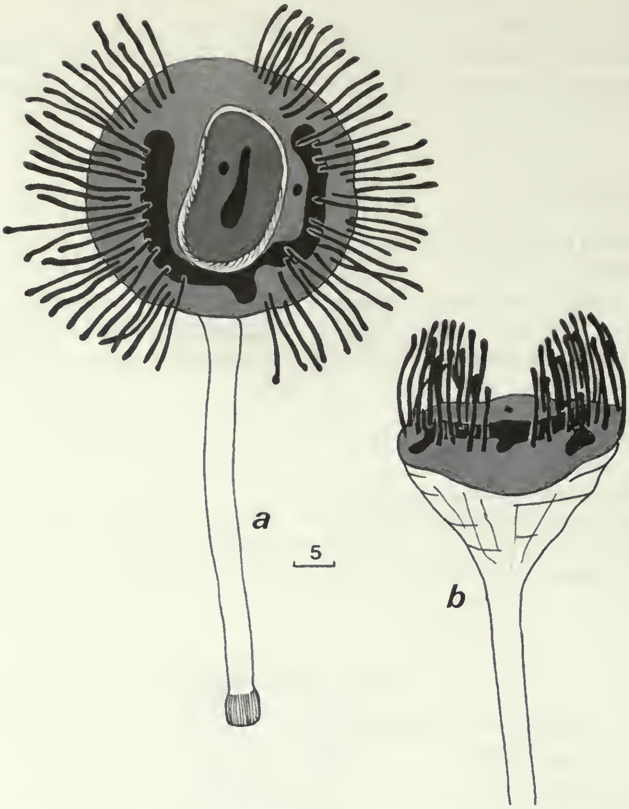

Fig. 13 *Pelagacineta interrupta*: (a,b) after Schröder, 1907 (called *Tokophrya interrupta*).

always elongate and highly branched. Reproduction by multiple endogenous budding producing oval swarmers partially ciliated with many kineties on part of the ventral body surface.

Pelagacineta dibdalteria (Parona, 1881), n. comb.

Acineta dibdalteria Parona, 1881

Description (Fig. 15). This is a small (50–60 μm long), marine suctorian with thecostyle. The body is pyriform in outline, rounded in cross section and lies at the top of a thecostyle that widens considerably to form a cupped lorica-like anterior region. Stalk region hollow, equal to or slightly less than the length of the lorica part of the thecostyle. There are only two capitate, prehensile mobile tentacles, one located anteriorly on either side of the body. Attached to marine algae. Contractile vacuole positioned centrally. Macronucleus elongate sausage-shaped. Reproduction and swarmers not described.

Pelagacineta euchaetae (Sewell, 1951) n. comb.

Acineta euchaetae Sewell, 1951

Description (Fig. 16). This is a medium (80–90 μm diameter), marine suctorian with thecostyle. The ovoid body lies at the top of a thecostyle that widens considerably to form a lorica-like anterior region. Young forms without lorica portion of the thecostyle. Stalk region hollow, usually shorter than length of the lorica part of the thecostyle, terminating in a longitudinally striated basal disc. Many retractile, capitate tentacles located anteriorly arranged in two fascicles. Attached to the

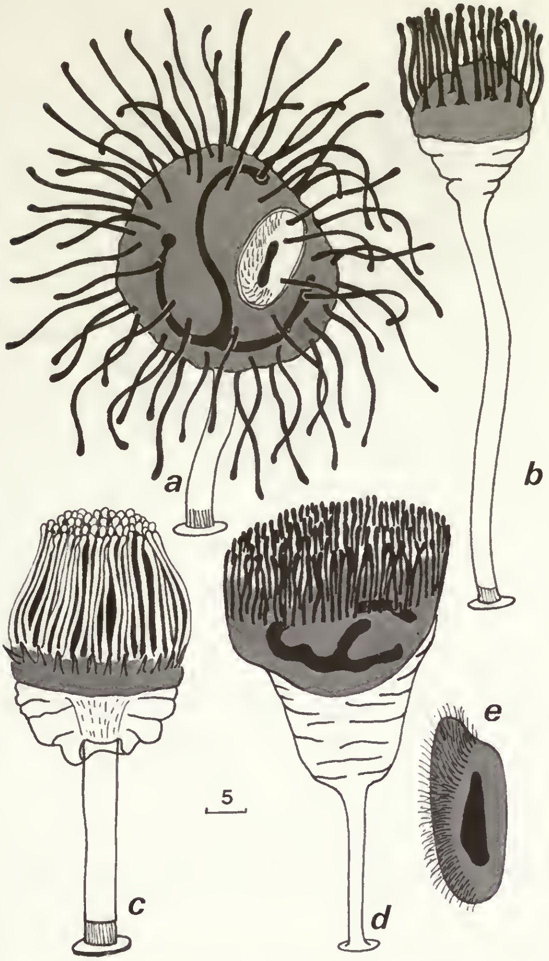

Fig. 14 *Pelagacineta campanula*: (a–c) after Schröder, 1907 (called *Tokophrya campanula*); (d,e) adult and swarmer, after Schröder, 1911 (called *Tokophrya steueri*).

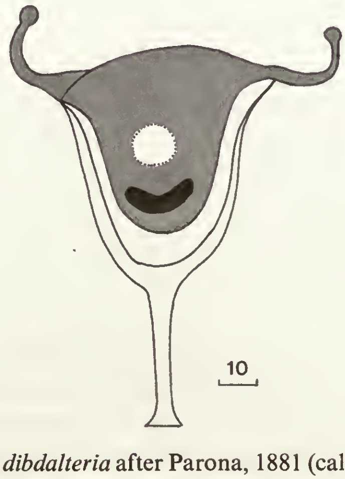

Fig. 15 *Pelagacineta dibdalteria* after Parona, 1881 (called *Acineta dibdalteria*).

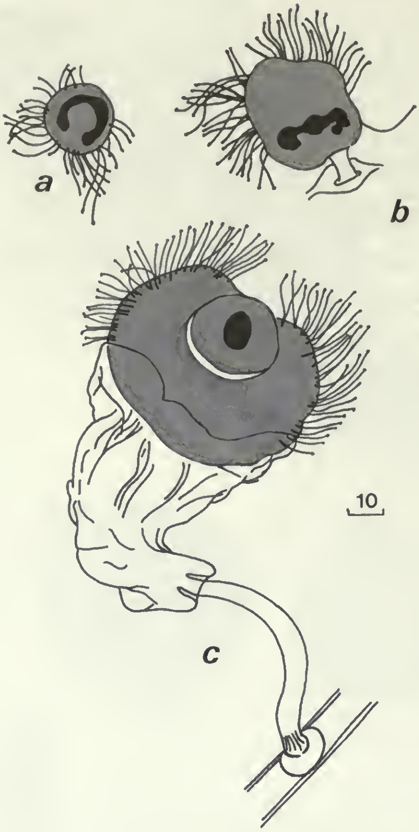

Fig. 16 *Pelagacineta euchaetae*: various growth stages, after Sewell, 1951 (called *Acineta euchaetae*).

marine copepod *Euchaeta* reported from antarctic waters. Shape of macronucleus variable, always elongate and curved. Reproduction by endogenous budding producing oval swarmers.

Genus ***PARACINETA*** Collin, 1911

Luxophrya Jankowski, 1978
Proluxophrya Jankowski, 1978
Stemacineta Jankowski, 1978

The genus *Paracineta* Collin, 1911 was erected in order to provide for those loricate suctoria with an apical group of tentacles that reproduced by external budding and were longitudinally symmetrical. The inclusion of *Paracineta crenata,* and *P. homari* which reproduce by semi-invaginative budding has already been dealt with above, but even after their removal, the species included by Collin (1912) in the genus *Paracineta* form a heterogenous group. Several other transfers have been suggested and are dealt with in other parts of this paper. After the removal of these from the genus the following four species remain from Collin's (1912) list, *Paracineta jorisi* (Sand, 1895), *P. limbata* (Maupas, 1881), *P. patula* (Claparède & Lachmann, 1861) and *P. vorticelloides* (Fraipont, 1878). Since that time, one other valid species has been added. One of the remaining major problems is the lack of a type species that will give some stability to the genus and enable a modern diagnosis to be proposed. This omission is rectified here by designating *Paracineta patula* (Claparède & Lachmann, 1861) Collin, 1911 as type species for the genus. This species is well described and includes good illustrated accounts of the budding and general morphology. Furthermore it is the only surviving species of the three originally placed in the genus by Collin (1911).

Diagnosis of *Paracineta*

Marine suctorians whose body shape is spherical to ovoid, rounded in transverse section. Long thecostyle with a semi-lorica that is variable in size. Semi-lorica may be sufficient to enclose half the zooid's volume or be reduced sufficiently for the body to be perched on top of a small cone-like widening at the top of the stem. Capitate tentacles usually restricted to apical body face but may radiate out from other areas when the semi-lorica is very small. Reproduction by exogenous budding, swarmers covered in many transverse ciliary rows.

Key to the species of *Paracineta*

1	Zooid perched on top of very small semi-lorica	2
	Approximately half of zooid enclosed within semi-lorica	4
2	Tentacles emerge from all over zooid	3
	Tentacles restricted to apical surface	***P. jorisi***
3	Zooid with thick gelatinous outer covering	***P. limbata***
	Zooid without gelatinous outer covering	***P. vorticelloides***
4	Stem of thecostyle with narrow flexible portion near junction with zooid	***P. patula***
	Stem of thecostyle not narrowed, not flexible	5
5	Thecostyle striated transversely regularly along entire length	***P. moebiusi***
	Thecostyle smooth, unstriated	6
6	Semi-lorica with border-like rim	***P. jorisi***
	Semi-lorica without border-like rim	7
7	Small, (semi-lorica 15–25 µm long), epizoic on polychaetes	***P. irregularis***
	Medium, (semi-lorica 30–80 µm long), epizoic on hydroids and marine algae	***P. patula***

Species descriptions

Paracineta patula (Claparède & Lachmann, 1861) Collin, 1911

Acineta patula Claparède & Lachmann, 1861
Acineta divisa Fraipont, 1878
Paracineta divisa Kahl, 1934
Stemacineta patula Jankowski, 1978

DESCRIPTION (Fig. 17). This the type species is a small (50–60 µm long), marine suctorian with a thecostyle. The ovoid to elongate body protrudes to a greater or lesser extent beyond the apical rim of thecostyle although the latter is sufficiently large to enclose at least half of the zooid. Capitate tentacles not in fascicles, usually covering the apical surface of the exposed part of the zooid. Apical part of thecostyle is triangular, tapering posteriorly to form a hollow tube-like stem that is at least three times the length of the lorica-like part. The junction between the two parts of the thecostyle often, secondarily, narrowed and flexible. Attached to hydroid colonies and marine algae. Single contractile vacuole usually positioned laterally. Spherical macronucleus located centrally. Reproduction by exogenous budding resulting in an ovoid swarmer covered in transverse ciliary rows with some anterior short residual tentacles.

NOTE. The observation by Collin (1912) that the formation of a narrow flexible junction between stem and lorica is a secondary event allows the inclusion of *Acineta divisa* Fraipont, 1878 as a junior synonym.

Paracineta irregularis Dons, 1928

DESCRIPTION (Fig. 18). This is a small (15–25 µm long), marine suctorian with a thecostyle. The ovoid to irregularly shaped body protrudes to a greater or lesser extent beyond the apical rim of thecostyle although the latter half of the zooid is always enclosed. Tentacles cover the apical

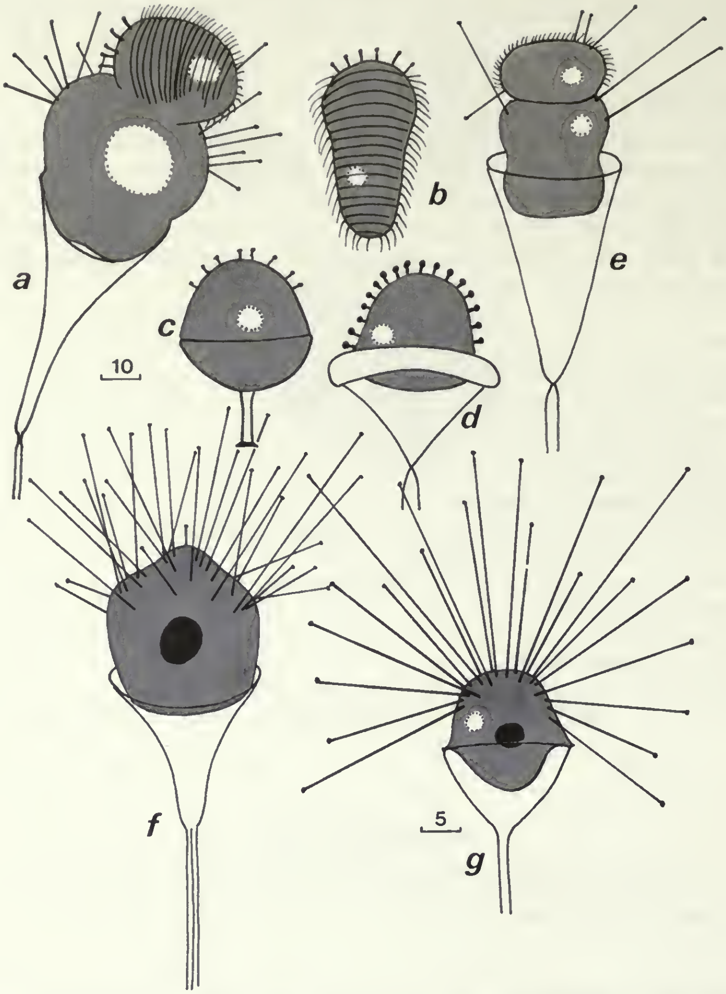

Fig. 17 *Paracineta patula*: (a–c) after Collin, 1912; (d–e) after Claparede & Lachmann, 1861 (called *Acineta patula*); (f) after Fraipont, 1877 (called *Acineta divisa*); (g) after Calkins, 1902 (called *Acineta divisa*).

surface of the exposed part of the zooid. Apical part of thecostyle irregularly triangular, tapering posteriorly to form a rigid hollow tube-like stem that is at least half the length of the lorica-like part. Epizoic on chaetae of the polychaete worm *Pherusa plumosa*. Spherical macronucleus located centrally. Reproduction not described.

Paracineta jorisi (Sand, 1895) Collin, 1912

Acineta jorisi Sand, 1895

Description (Fig. 19). This is a small to medium (30–80 µm long), marine suctorian with a thecostyle. The ovoid to pyriform body protrudes to a great extent beyond the apical rim of the semi-lorica part of the thecostyle which is not normally large enough to enclose the zooid. Tentacles not in fascicles, usually covering the apical surface of the exposed part of the body. Apical part of thecostyle is triangular or cup-like. The rim is prominently flared and folds back on itself to form an internal layer upon which the zooid is mounted. Thecostyle tapers posteriorly to

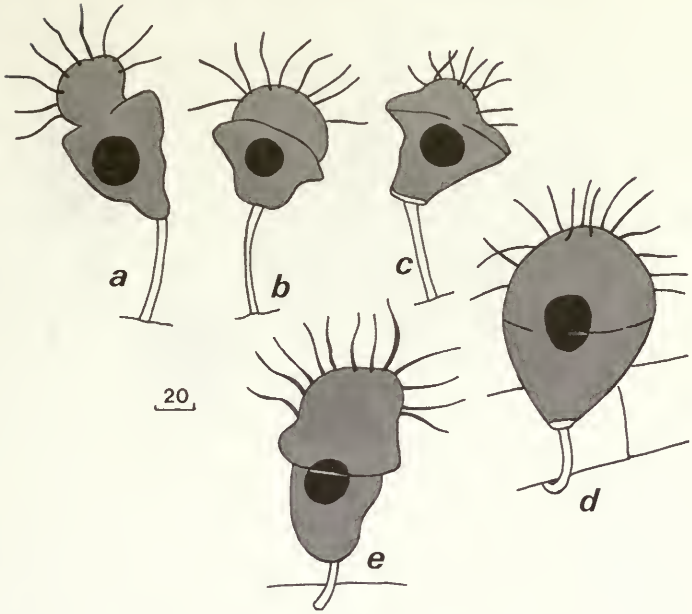

Fig. 18 *Paracineta irregularis*: (a–e) various forms after Dons, 1928.

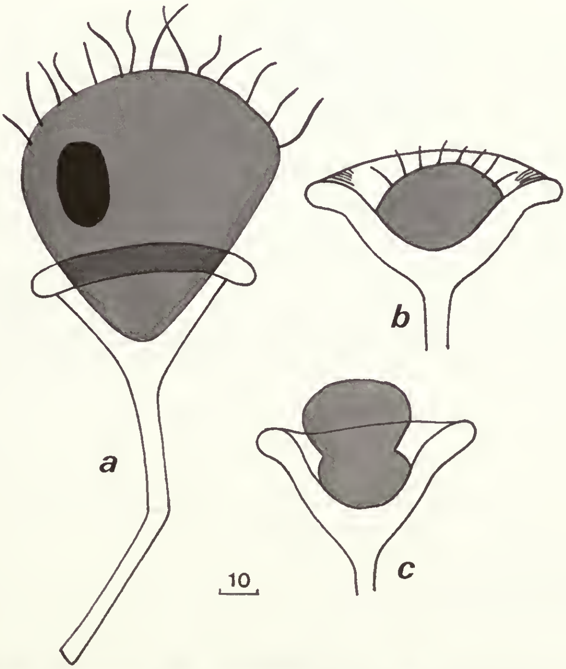

Fig. 19 *Paracineta jorisi* after Sand, 1895 (called *Acineta jorisi*).

form a rigid hollow tube-like stem that is at least three times the length of the lorica-like part. Attached to hydroid colonies such as *Vesicularia* and *Sertularia*. Single contractile vacuole. Spherical macronucleus located centrally. Reproduction by exogenous budding.

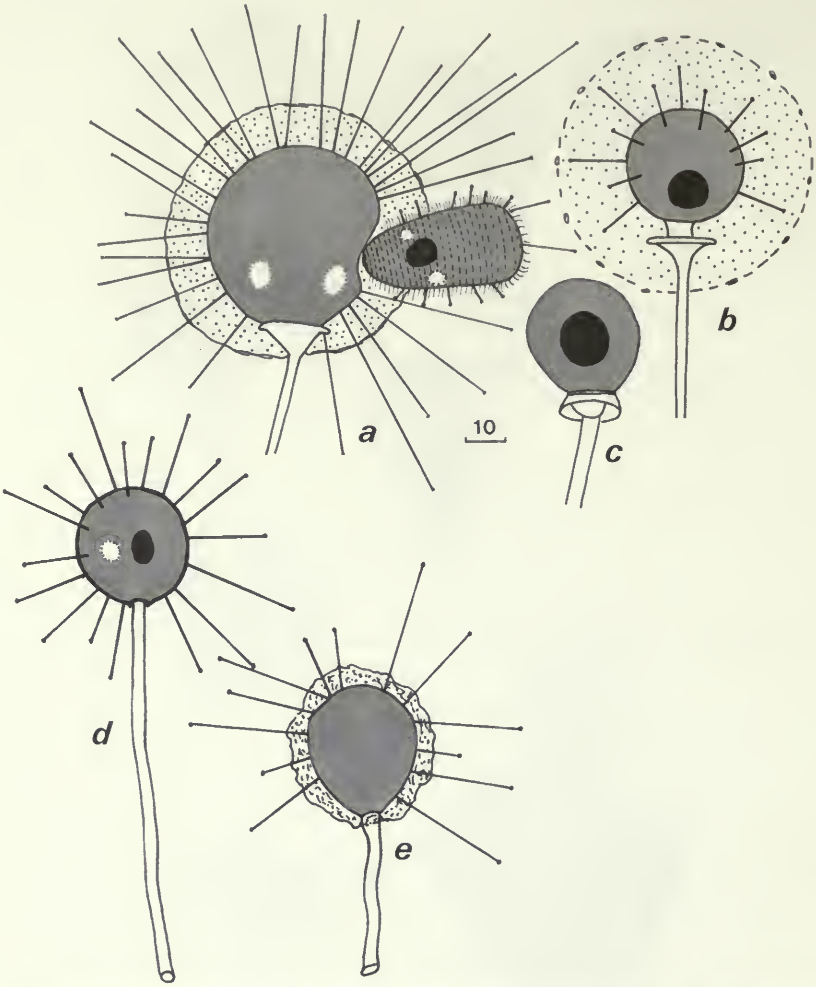

Fig. 20 *Paracineta limbata*: (a) adult with swarmer, after Collin, 1912; (b) after Wailes, 1928; (c) after Dons, 1922; (d,e) after Moebius, 1888 (called *Podophrya limbata*).

Paracineta limbata (Maupas, 1881) Collin, 1912

Podophrya limbata Maupas, 1881
Tokophrya limbata Bütschli, 1889
Paracineta limbata forma *convexa* Dons, 1922
Luxophrya limbata Jankowski, 1978

DESCRIPTION (Fig. 20). This is a small (20–45 µm diameter), marine suctorian with a thecostyle. The spherical body is mounted on the rim of a greatly reduced lorica-like part of the thecostyle. Zooid often covered by a thick gelatinous outer coat. Capitate tentacles not in fascicles, radiate out from the entire surface of the exposed zooid. Reduced apical part of thecostyle is cone-like, tapering posteriorly to join a rigid hollow tube-like stem that is at least four times the diameter of the zooid in length. Attached to hydroid colonies. Two contractile vacuoles usually positioned laterally. Spherical macronucleus located centrally. Reproduction by exogenous budding resulting in an ovoid swarmer covered in transverse ciliary rows with some residual tentacles.

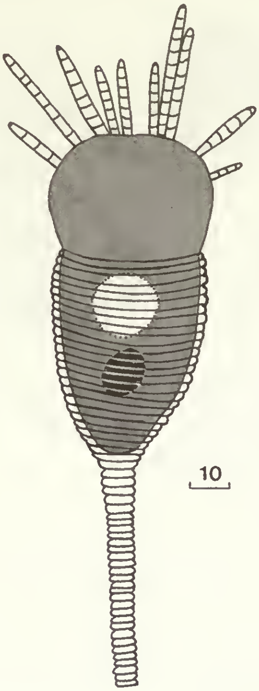

Fig. 21 *Paracineta moebiusi* after Moebius, 1888 (called *Acineta crenata*).

Paracineta moebiusi (Moebius, 1888) Kahl, 1934

Acineta crenata Moebius, 1888

DESCRIPTION (Fig. 21). This is a medium (76 µm long), marine suctorian with a thecostyle. Approximately half the elongate body protrudes beyond the apical rim of thecostyle. Tentacles not in fascicles, covering only the apical surface of the exposed part of the zooid. The thecostyle is prominently and totally ribbed transversely. The apical part is cup-shaped, and tapers posteriorly to form a rigid hollow tube-like stem that is about one and a half times the length of the lorica-like part. Epizoic on the crustacean *Holocarus*. Single anterior contractile vacuole. Spherical macronucleus located posteriorly. Reproduction not described.

Paracineta vorticelloides (Fraipont, 1877) Collin, 1912

Acineta vorticelloides Fraipont, 1877
Proluxophrya vorticelloides Jankowski, 1978

DESCRIPTION (Fig. 22). This is a small (30–40 µm diameter), marine suctorian with a thecostyle. The spherical body is mounted on the greatly reduced anterior part of the thecostyle. Capitate tentacles not in fascicles, radiating out from the entire surface of the exposed zooid. Reduced apical part of thecostyle is cup-like, tapering posteriorly to join a rigid hollow tube-like stem that is at least four times the diameter of the body in length. Epizoic on hydroid colonies, crustacea and marine algae. Single central contractile vacuole. Spherical macronucleus located posteriorly. Reproduction by exogenous budding.

Genus *LORICOPHRYA* Matthes, 1956

Acineta Ehrenberg, 1833 *pro parte*
Thecacineta Collin, 1909 *pro parte*
Paracineta Collin, 1911 *pro parte*

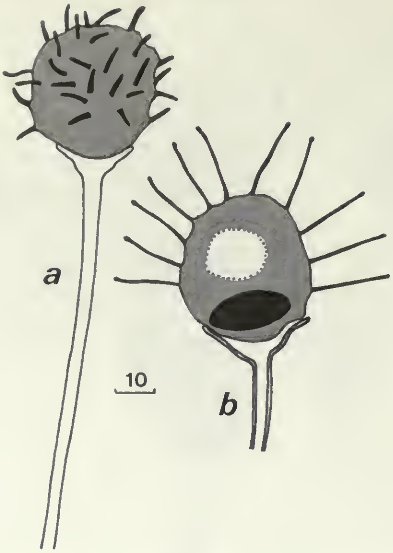

Fig. 22 *Paracineta vorticelloides*: (a,b) after Fraipont, 1878 (called *Acineta vorticelloides*).

Corynacineta Jankowski, 1978
Heliotheca Jankowski, 1978
Paraloricophrya Jankowski, 1978
Spongiophrya Jankowski, 1978

The genus was originally erected by Matthes (1956) for loricate suctoria with a single apical group of tentacles but with an unknown method of budding. He designated *Loricophrya parva* (Schulz, 1932) as the type species and listed the following species to constitute the genus: *Loricophrya cattanei* (Parona, 1883), *L. simplex* (Maskell, 1886), *L. lasanicola* (Maskell, 1887), *L. tulipa* (Maskell, 1887), *L. solenophryaformis* (Sand, 1899), *L. cypridinae* (Collin, 1912), *L. caepula* (Penard, 1920), *L. edmondsoni* (King, 1932), *L. sivertseni* (Allgén, 1951), *L. trichophora* (Allgén, 1951) and *L. longe-petiolatus* (Allgén, 1951). The present author does not consider all of these species to be congeneric although the majority are retained in this revision. The three species described by Maskell (1886, 1887) have already been transferred back (Curds, 1985) into the genus *Acineta* but the generic position of *L. cattanei* (Parona, 1883) is still uncertain. Similarly, *L. cypridinae* (Collin, 1912) will be returned back to its original genus *Thecacineta*. All the others in Matthes (1956) original list have been retained within the genus although the specific epithet may be different to that used by him and several additions have been made.

Diagnosis of *Loricophrya*

Freshwater or marine sectoria with a thecostyle. When clearly differentiated the stem is shorter than the lorica part of the thecostyle. Body ovoid to elongate, rounded in cross-section. Capitate tentacles restricted to a single group on the apical surface of the zooid. Mode of reproduction not yet recorded.

Key to the species of *Loricophrya*

1	Thecostyle continually narrows posteriorly without a stalk region being clearly differentiated	2
	A narrow stalk region is clearly differentiated from the rest of the thecostyle	4
2	Most of zooid projects out of short thecostyle	***L. oviformis***
	Most of zooid enclosed within long thecostyle	3
3	Zooid small, pyriform, lying in apical quarter of thecostyle	***L. tuba***
	Zooid large, elongate, filling most of thecostyle cavity	***L. sivertseni***

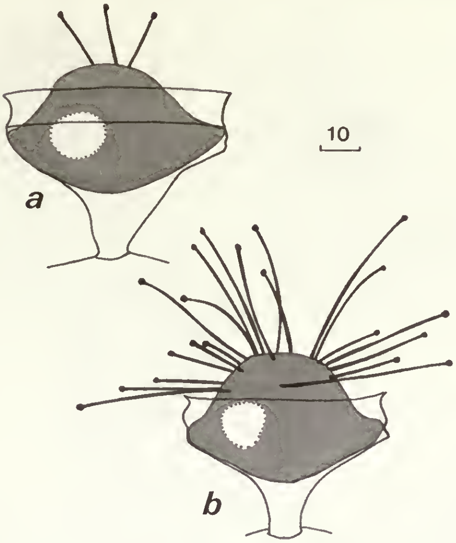

Fig. 23 *Loricophrya parva*: (a,b) after Schulz, 1932 (called *Thecacineta parva*).

4	Zoid longer than wide, never dorso-ventrally flattened nor discoidal.	5
	Zooid wider than length, flattened dorso-ventrally or discoidal in shape	9
5	Lorica part of thecostyle striated transversely	***L. lauterborni***
	Lorica part of thecostyle without striations or ribs	6
6	Thecostyle wider than height, covered in tubercles	***L. bifaria***
	Thecostyle longer than wide, smooth	7
7	Stalk part of thecostyle is half length of lorica part, and may be striated	8
	Stalk part of thecostyle very short, about 1/8 of lorica part, not striated	***L. multitentaculata***
8	Stalk part of thecostyle striated, lorica part triangular in outline	***L. stresemanni***
	Stalk part of thecostyle not striated, lorica part oval in outline	***L. trichophora***
9	Stalk region very short, about 1/8 length of lorica region. Rim without collar, small aperture	***L. caepula***
	Stalk region short, about 1/2 length of lorica region. Rim of thecostyle with collar region surrounding wide aperture	10
10	Stalk part of thecostyle conical in shape	***L. parva***
	Stalk part of thecostyle tubular	***L. solenophryaformis***

Species descriptions

Loricophrya parva (Schulz, 1932) Matthes, 1956

Thecacineta parva Schulz, 1932

DESCRIPTION (Fig. 23). This the type species is a small (36–41 μm long), brackish-water suctorian with a thecostyle. The discoidal body is rounded in cross-section and lies within an urn-like thecostyle. There is a single apical group of capitate tentacles on the apical surface. The thecostyle narrows somewhat posteriorly to form a cone-like stalk region. Attached to inanimate objects. Single lateral contractile vacuole. Macronucleus oval, centrally located. Reproduction not described.

Loricophrya bifaria (Stokes, 1887) n. comb.

Acineta bifaria Stokes, 1887
Paracineta bifaria Collin, 1912
Paraloricophrya bifaria Jankowski, 1978

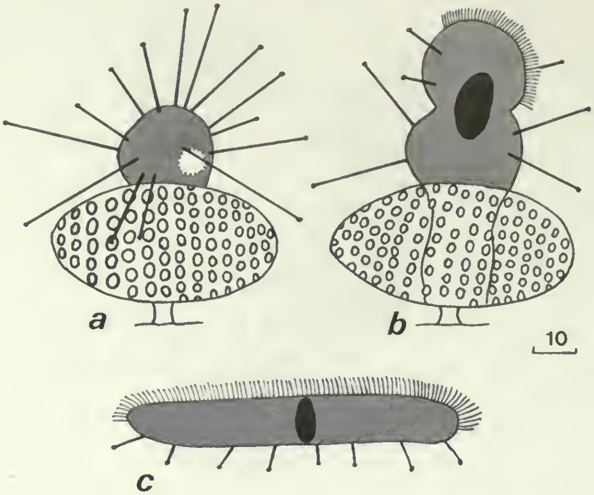

Fig. 24 *Loricophrya bifaria*: (a) adult; (b) budding; (c) swarmer; all after Stokes, 1887 (called *Acineta bifaria*).

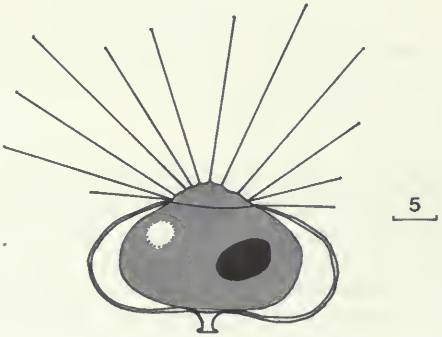

Fig. 25 *Loricophrya caepula* after Penard, 1920 (called *Thecacineta caepula*).

Description (Fig. 24). This is a small (45 µm diameter), freshwater suctorian with a thecostyle. The elongate body is rounded in cross-section and projects out well beyond the rim of the thecostyle. There is a single group of apical capitate tentacles. Stalk region a short, button-like projection. Lorica region ovoid, covered in tubercles, width greater than height. Single lateral contractile vacuole. Ovoid macronucleus centrally located. Reproduction by exogenous budding resulting in an elongate swarmer with longitudinal rows of cilia and some residual tentacles.

Loricophrya caepula (Penard, 1920) Matthes, 1956

Thecacineta caepula Penard, 1920
Heliotheca caepula Jankowski, 1978

Description (Fig. 25). This is a small (33 µm diameter), freshwater suctorian with a thecostyle. The ovoid body is rounded in cross-section and just projects out beyond the rim of the thecostyle. There is a single group of apical capitate tentacles. Stalk region a short, button-like projection. Lorica region ovoid, width greater than height. Single anterio–lateral contractile vacuole. Ovoid macronucleus centrally located. Reproduction not described.

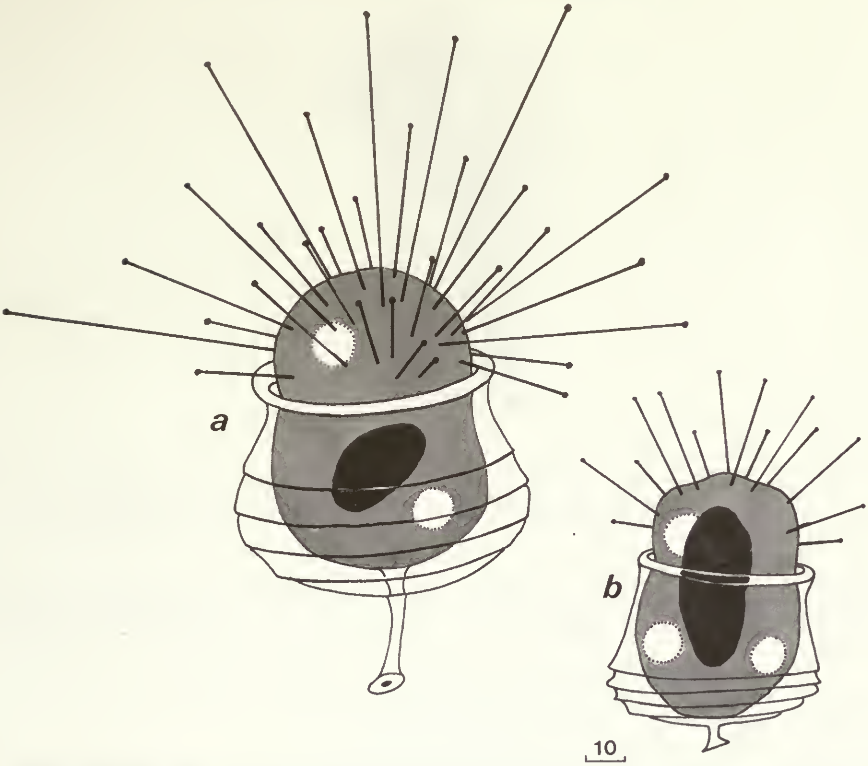

Fig. 26 *Loricophrya lauterborni*: (a) after Sondheim, 1929 (called *Paracineta lauterborni*); (b) after King, 1932 (called *Thecacineta edmondsi*).

Loricophrya lauterborni (Sondheim, 1929) n. comb.

Paracineta lauterborni Sondheim, 1929
Thecacineta edmondsi King, 1932
Paraloricophrya lauterborni Jankowski, 1978

Description (Fig. 26). This is a small (40–55 µm diameter), freshwater suctorian with a thecostyle. The ovoid body is rounded in cross-section and projects out beyond the rim of the thecostyle. Capitate tentacles radiate out from the surface of the exposed part of the zooid. Stalk region a short, button-like projection or up to half the lorica length. Lorica region cup-like with about four transverse rings. Attached to inanimate objects. Two or three contractile vacuoles. Ovoid macronucleus centrally located. Reproduction possibly by exogenous budding.

Loricophrya multitentaculata (Sand, 1895) n. comb.

Hallezia multitentaculata Sand, 1895
Acineta multitentaculata Sand, 1899
Paracineta multitentaculata Collin, 1912
Spongiophrya multitentaculata Jankowski, 1978

Description (Fig. 27). This is a large (304 µm long), marine suctorian with a thecostyle. The cylindrical body is rounded in cross-section and only the small posterior part is housed in the cup-like thecostyle. There is a single apical group of capitate tentacles on the apical surface. The thecostyle follows the outline of the body and there is a short button-like stalk region. Epizoic on sponges such as *Leucosolenia*. Contractile vacuole not observed. Macronucleus large, elongate, centrally located. Reproduction not described.

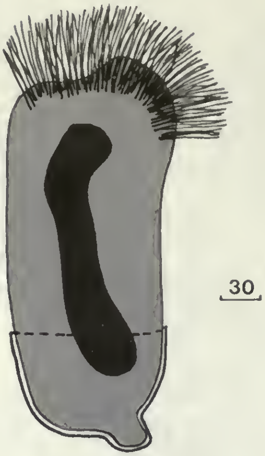

Fig. 27 *Loricophrya multitentaculata* after Sand, 1895 (called *Hallezia multitentaculata*). Note that the theca was described but not illustrated in the original description.

NOTE. The presence of a lorica was not shown in the diagram of this species but was mentioned clearly in the description. Here the presence of a lorica is indicated means of dotted lines.

Loricophrya oviformis (Dons, 1918) n. comb.

Paracineta oviformis Dons, 1918

DESCRIPTION (Fig. 28). This is a medium (85 µm long), marine suctorian with a thecostyle. The ovoid body is only partially enclosed within the thecostyle whose rim is smooth. There is a single group of tentacles which are scattered over much of the exposed body surface. The thecostyle follows the outline of the body posterior and there is a short button-like stalk-region. Epizoic on the worm *Spirorbis*. Nuclear and reproductive features not described.

Loricophrya sivertseni (Allgén, 1951) Matthes, 1956

Thecacineta sivertseni Allgén, 1951

DESCRIPTION (Fig. 29). This is a large (108 µm long), marine suctorian with a thecostyle. The elongate body is totally enclosed within the cone-shaped thecostyle whose rim is scalloped.

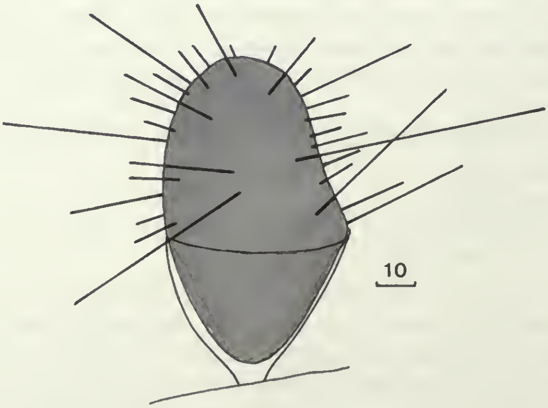

Fig. 28 *Loricophrya oviformis* after Dons, 1918 (called *Paracineta oviformis*).

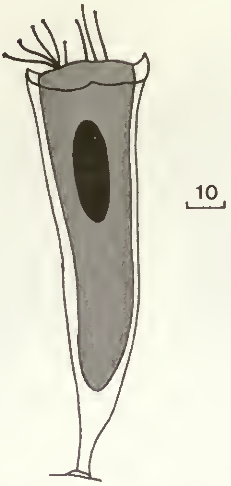

Fig. 29 *Loricophrya sivertseni* after Allgén, 1951 (called *Thecacineta sivertseni*).

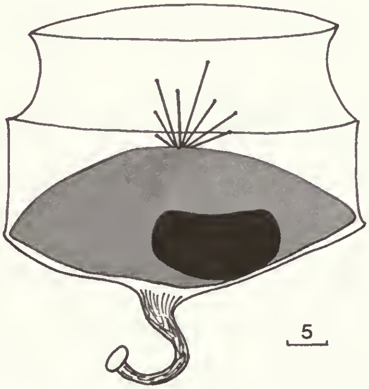

Fig. 30 *Loricophrya solenophryaformis* after Sand, 1899 (called *Acineta solenophryaformis*).

Capitate tentacles in a single apical group. There is no distinct stalk region, the lorica gradually and continually narrows posteriorly to join the attachment plate. Epizoic on the nematode worm *Spirina parasitifera*. Ovoid macronucleus centrally located. Mode of reproduction not described.

Loricophrya solenophryaformis (Sand, 1899) Matthes, 1956

Acineta solenophryaformis Sand, 1899
Thecacineta solenophryaformis Collin, 1909

DESCRIPTION (Fig. 30). This is a small (30–35 µm long), freshwater suctorian with a thecostyle. The discoid body is totally enclosed within an urn-like thecostyle whose rim is surrounded by a collar-like region. Capitate tentacles located in a single, tightly-packed, apical group which are enclosed within the thecostyle. There is a short but distinct, tubular stalk region. Attached to freshwater algae. Ovoid macronucleus located posteriorly. Mode of reproduction not described.

Loricophrya stresemanni (Allgén, 1951) Matthes, 1956

Paracineta stresemanni Allgén, 1951

DESCRIPTION (Fig. 31). This is a small (40 µm long), marine suctorian with a thecostyle. The

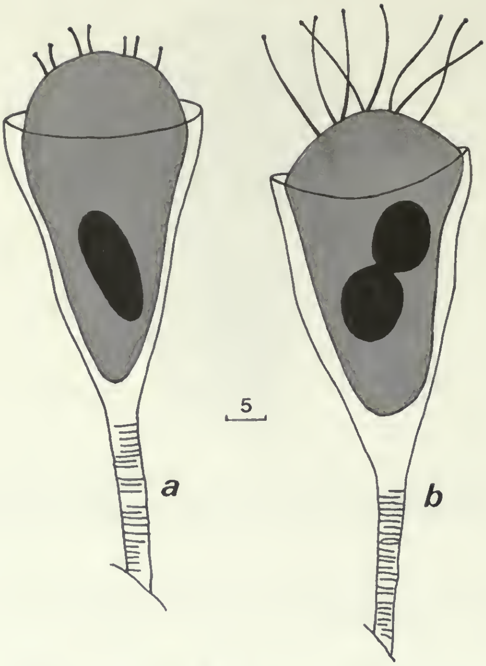

Fig. 31 *Loricophrya stresemanni*: (a,b) after Allgén, 1951 (called *Paracineta stresemanni*).

elongate body is mostly enclosed within a cone-shaped thecostyle whose rim is smooth. Capitate tentacles in a single apical group. There is a distinct stalk region which is about half the lorica length and is striated transversely. Epizoic on the nematode worm *Spirina parasitifera*. Ovoid macronucleus centrally located. Mode of reproduction not described.

Loricophrya trichophora (Allgén, 1951) Matthes, 1956

Thecacineta trichophora Allgén, 1951
Thecacineta longe-petiolatus Allgén, 1951

Description (Fig. 32). This is a medium (80 µm long), marine suctorian with a thecostyle. The elongate body is totally enclosed within an ovoid thecostyle whose rim is smooth. Capitate tentacles in a single apical group. There is a distinct stalk region which is about half the lorica length, not striated. Epizoic on the nematode worm *Spirina parasitifera*. Ovoid macronucleus centrally located. Mode of reproduction not described.

Loricophrya tuba (Zelinka, 1914) n. comb.

Acineta tuba Zelinka, 1914
Paracineta tuba Kahl, 1934
Corynacineta tuba Jankowski, 1978

Description (Fig. 33). This is a small (25–32 µm long), marine suctorian with a thecostyle. The pyriform body is enclosed within the apical quarter of the elongated cone-like thecostyle. Tentacles emerge from the apical surface, not in fascicles. There is no distinct stalk region, the lorica gradually and continually narrows posteriorly to join the substratum. Epizoic on the shells of echinoderms. Ovoid macronucleus centrally located. Mode of reproduction not described.

Genus *ANTHACINETA* Jankowski, 1978

Acineta Ehrenberg, 1833 *pro parte*
Noracineta Jankowski, 1978

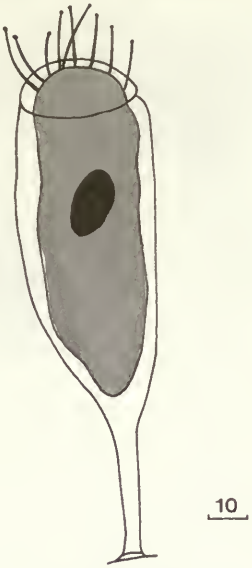

Fig. 32 *Loricophrya trichophora* after Allgén, 1951 (called *Paracineta trichophora*).

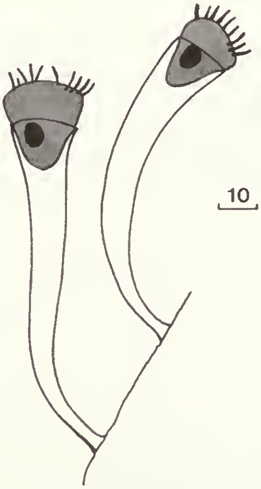

Fig. 33 *Loricophrya tuba* after Zelinka, 1914 (called *Acineta tuba*).

The genus *Anthacineta* was erected by Jankowski (1978) for *Acineta craterellus* Collin, 1909 giving the following brief diagnosis 'semi-lorica – stylotheca'. According to that brief definition the genus could be transferred to *Paracineta* and several other similar genera as a junior synonym. It can only be classified as a distinct genus if the two fascicles of tentacles and rounded transverse section to the body are taken into account. Here the diagnosis has been expanded and one other species, *Acineta infundibuliformis* Wang & Nie, 1933, has been transferred to it for the first time.

Diagnosis of *Anthacineta*

Marine suctorians with thecostyle. Zooid only partly enclosed in the semi-lorica part of the thecostyle which has a long stem. Body ovoid, rounded in cross-section. Two fascicles of capitate tentacles present, one either side of the zooid. Mode of reproduction not recorded.

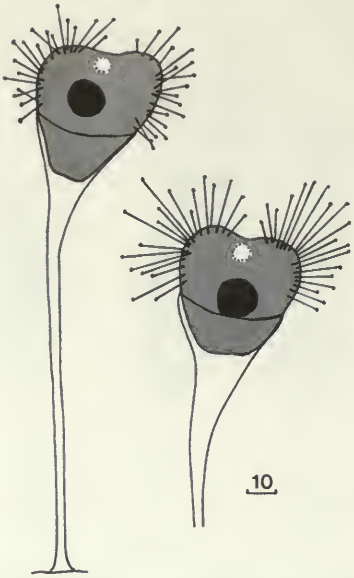

Fig. 34 *Anthacineta craterellus* after Collin, 1912 (called *Acineta craterellus*).

Key to the species of *Anthacineta*

1 Zooid wider than long, contractile vacuole in posterior body half. Thecostyle narrows abruptly to form stalk-like region . . . . ***A. infundibuliformis***

Zooid longer than wide, contractile vacuole in anterior body half. Thecostyle narrows consistently to form the stalk-like region . . . . ***S. craterellus***

Species descriptions

Anthacineta craterellus (Collin, 1909) Jankowski, 1978

Acineta tuberosa Sand, 1901 *pro parte*
Acineta craterellus Collin, 1909

Description (Fig. 34). This the type species is a small (50 µm long), marine suctorian with a thecostyle. The ovoid to pyriform body is rounded in cross-section and about half of it protrudes beyond the rim of the semi-lorica part of the thecostyle. There are two anterio–lateral fascicles of capitate tentacles. The lorica part of the thecostyle is short and cone-like, narrowing gently posteriorly to form the hollow stem region that is at least twice the length of the zooid. Epizoic on bryozoa. Single contractile vacuole situated apically between fascicles. Spherical macronucleus centrally located. Reproduction not described.

Anthacineta infundibuliformis (Wang & Nie, 1933) n. comb.

Acineta infundibuliformis Wang & Nie, 1933
Noracineta infundibuliformis Jankowski, 1978

Description (Fig. 35). This is a small (50 µm long), marine suctorian with a thecostyle. The wedge-shaped body is rounded in cross-section and about half of it protrudes beyond the rim of the semi-lorica part of the thecostyle. There are two lateral fascicles of capitate tentacles. The lorica part of the thecostyle is short and cone-like, narrowing abruptly posteriorly to form the hollow stem region that is about the length of the lorica. Attached to marine algae. Single contractile vacuole situated posteriorly. Ovoid macronucleus centrally located. Reproduction not described.

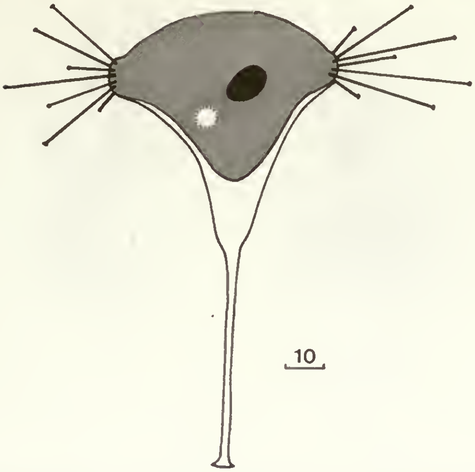

Fig. 35 *Anthacineta infundibuliformis* after Wang & Nie, 1933 (called *Acineta infundibuliformis*).

Genus *FLECTACINETA* Jankowski, 1978

Acineta Ehrenberg, 1833 *pro parte*
Podophrya Ehrenberg, 1833 *pro parte*
Alderia Alder, 1851
Paracineta Collin, 1911 *pro parte*

The genus was erected by Jankowski (1978) for *Acineta livadiana* Mereschowsky, 1881 who gave the following brief diagnosis, 'with stylotheca and apical tentacles'. The stalk is normally shown as being hollow but not as an extension of the lorica as the term stylotheca implies. Thus the diagnosis has been emended slightly and expanded for the sake of clarity. Two species *Paracineta dadyi* (Daday, 1886) Kahl, 1934 and *Acineta elegans* Imhoff, 1883 have been transferred to the genus for the first time.

Diagnosis of *Flectacineta*

Marine loricate suctorians. Ovoid body, rounded in cross-section lying within lorica. Capitate tentacles restricted to single apical group. Thecostyle lorica rim characteristically inverted at apex, mounted upon a hollow stalk. Reproduction by exogenous budding.

Key to the species of *Flectacineta*

1	Rim of lorica smooth, junction between stalk and lorica simple	2
	Rim of lorica scalloped, junction between stalk and lorica complex	***F. elegans***
2	Wall or lorica divided into an inner and outer wall near aperture	***F. dadyi***
	Wall of lorica not divided	***F. livadiana***

Species descriptions

Flectacineta livadiana (Mereschkowsky, 1881) Jankowski, 1978

Cothurnia havniensis Ehrenberg, 1838
Alderia pyriformis Alder, 1851
Podophrya pyriformis Pritchard, 1861
Acineta livadiana Mereschkowsky, 1881
Acineta neapolitana Daday, 1886
Acineta sp. Robin, 1879
Paracineta neapolitana Kahl, 1934

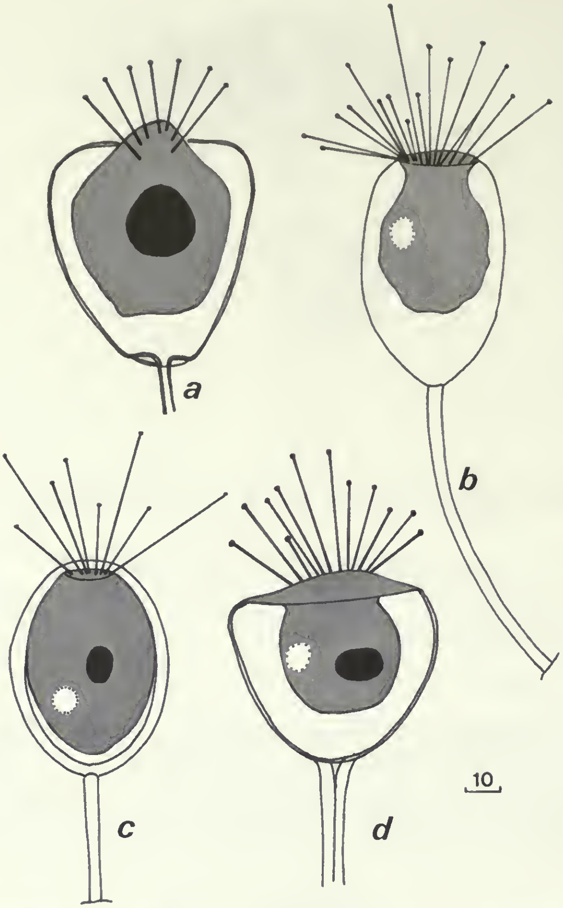

Fig. 36 *Flectacineta livadiana*: (a) after Sand, 1895 (called *Acineta livadiana*); after Mereschkowsky, 1881 (called *Acineta livadiana*); (c) after Wang & Nie, 1933 (called *Acineta livadiana*); (d) after Daday, 1886 (called *Acineta neapolitana*).

Description (Fig. 36). This the type species is a small to medium (30–80 µm long), marine, loricate suctorian. The small ovoid body is rounded in cross-section and is completely enclosed within the lorica. There is a single apical group of capitate tentacles. The lorica is ovoid with an inverted rim that forms a small aperture. The stem region is distinct and most diagrams show that there is usually at least a narrow channel through the centre. Length of stem variable. Epizoic on hydroids and marine algae. Single contractile vacuole situated laterally. Ovoid macronucleus centrally located. Reproduction by exogenous budding.

Flectacineta dadayi (Daday, 1886) n. comb.

Acineta livadiana Daday, 1886
Paracineta livadiana Collin, 1912 *pro parte*
Paracineta dadayi Kahl, 1934

Description (Fig. 37). This is a small (45 µm long), marine, loricate suctorian. The small ovoid body is rounded in cross-section and is completely enclosed within the lorica. There is a single apical group of capitate tentacles. The lorica is ovoid to cone-shaped with an inverted rim that forms a small aperture. The lorica surrounding the aperture is divided into an inner and an outer wall. The hollow stem region is distinct and some diagrams show that there is a narrow

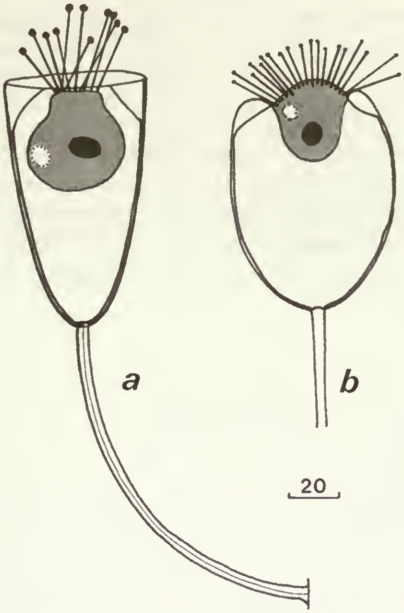

Fig. 37 *Flectacineta dadayi*: (a) after Daday, 1886 (called *Acineta livadiana*); (b) after Collin, 1912 (called *Paracineta livadiana*).

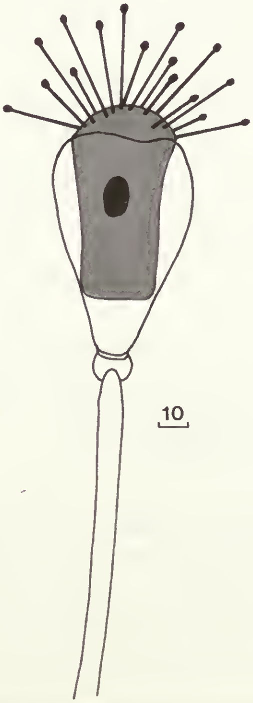

Fig. 38 *Flectacineta elegans* after Imhoff, 1884 (called *Acineta elegans*).

channel through the centre. Length of stem region about that of lorica. Epizoic on hydroids and marine algae. Single contractile vacuole situated laterally. Ovoid macronucleus centrally located. Reproduction not described.

Flectacineta elegans (Imhoff, 1883) n. comb.

Acineta elegans Imhoff, 1883 *non* Maskell, 1886
Paracineta elegans Collin, 1912

DESCRIPTION (Fig. 38). This is a medium (70 µm long), marine, loricate suctorian. The rectangular body is rounded in cross-section and is completely enclosed within the lorica. There is a single apical group of capitate tentacles. The lorica is pyriform with an inverted scalloped rim that forms a small aperture. The hollow stem region is distinct and joins the lorica via an intervening ball-like joint. Length of stem at least twice that of the lorica. Epizoic on the cladoceran *Bythotrephes longimanus*. Single apical contractile vacuole. Ovoid macronucleus centrally located. Reproduction not described.

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British Museum (Natural History)

An Atlas of Freshwater Testate Amoebae

C. G. Ogden & R. H. Hedley

1980, Hardcovers, 222pp, £17.50 (£18.00 by post) Co-published by British Museum (Natural History) and Oxford University Press.

This book illustrates, using scanning electron micrographs, most of the common species of testate amoebae that are found in freshwater habitats. Information on the biology, ecology, geographical distribution and a classification are followed by descriptions of ninety-five species. Each of these is illustrated by several views of the shell. The text if designed not only to enable biologists to identify species of testate amoebae, but to serve as an introduction to students interested in the taxonomy and biology of these freshwater protozoa. It will be of special interest to protozoologists, ecologists, limnologists, water treatment specialists and micropalaeontologists interested in recent sediments.

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Notes on spiders of the family Salticidae. 1. The genera *Spartaeus*, *Mintonia* and *Taraxella*

F. R. Wanless

Zoology series Vol 52 No 3 26 March 1987

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Notes on spiders of the family Salticidae.
1. The genera *Spartaeus*, *Mintonia* and *Taraxella*

F. R. Wanless
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

The genus *Taraxella* is redefined to include those spartaeines in which the embolus of the male palp is largely obscured by tegular apophyses. The male of *Spartaeus thailandica* Wanless and the female of *Mintonia melinauensis* Wanless are described for the first time. One new species of *Spartaeus,* two new species of *Mintonia* and four new species of *Taraxella* are described from the Oriental Region. Diagnoses and figures are provided. The presence of mytiliform organs on the legs and filamentous metatarsal leg fringes are described for the first time. They are illustrated, together with femoral organs, muscle attachment sites and apophyses by scanning electron micrographs.

Introduction

The purpose of the present paper is to describe seven new species and the previously unknown male and female of two described species belonging in the subfamily Spartaeinae. The subfamily is of particular interest because some species spin large webs that are used to capture prey. Typical salticids are cursorial hunters with good vision that do not spin webs to capture prey, although they will spin silk nests in which to lay eggs, moult and sometimes mate, and generally rest at night or during other periods of inactivity (Jackson, 1979).

The first reports of web-spinning in jumping spiders (Coleman, 1978, 1980; Murphy, *in* Wanless, 1978*b*) were followed by several important studies (Jackson & Blest, 1982; Jackson, 1982; Jackson & Hallas, in press a) that confirmed the phenomenon and provided a rare insight into the biology of a small group of tropical salticids. These spiders all belonged in the old world genus, *Portia* Karsch, that is presently classified along with 12 other genera in the subfamily Spartaeinae. In addition to building large prey-capture webs, *Portia* species will leave their web and stalk prey as cursorial hunters i.e. in the same manner as other salticids. Furthermore, they may invade the webs of other spiders and feed on trapped insects (kleptoparasitism), the resident spider, or even its eggs (oophagy). In life they resemble tatty mouldy leaves or detritus, their ornate hair tufts and fringes (Fig. 3) providing a form of camouflage that enables them to stalk prey without being noticed, an important guise since they show a marked preference for other spiders, including salticids. *Portia* species are also 'aggressive vibratory mimics' for when they invade other spider webs they pluck the threads and deceive the owner into accepting *Portia* as potential prey only to be attacked themselves on approaching within jumping distance.

Occurrence of the unusual behaviour patterns of *Portia* species correlate to some degree in this and related spartaeines by the presence of morphological structures that are not known to occur in other spiders. These include femoral organs (Figs 5E; 14A) and pore-bearing apophyses (Figs 9E arrowed; 20A, B) both of which are especially evident in some of the species described below. Also present on the legs of one species (*Spartaeus wildtrackii* sp. n.) are mytiliform organs (Fig. 15A–C; 16A, B), structures that have hitherto only been found grouped together as a discrete patch on the dorsal surface of the abdomen (Fig. 20C) of species of *Cyrba* Simon, *Portia, Gelotia* Thorell, and *Mintonia* Wanless. The function of these structures is unknown but previous studies (Wanless, 1984a, b; 1985) have suggested that they may be associated with pheromone dispersal. Jackson & Hallas (in press *b*) have demonstrated that sex pheromones are involved in mate recognition in some *Portia, Brettus* Thorell and *Cyrba,* thus supporting earlier work by Legendre and Llinares,

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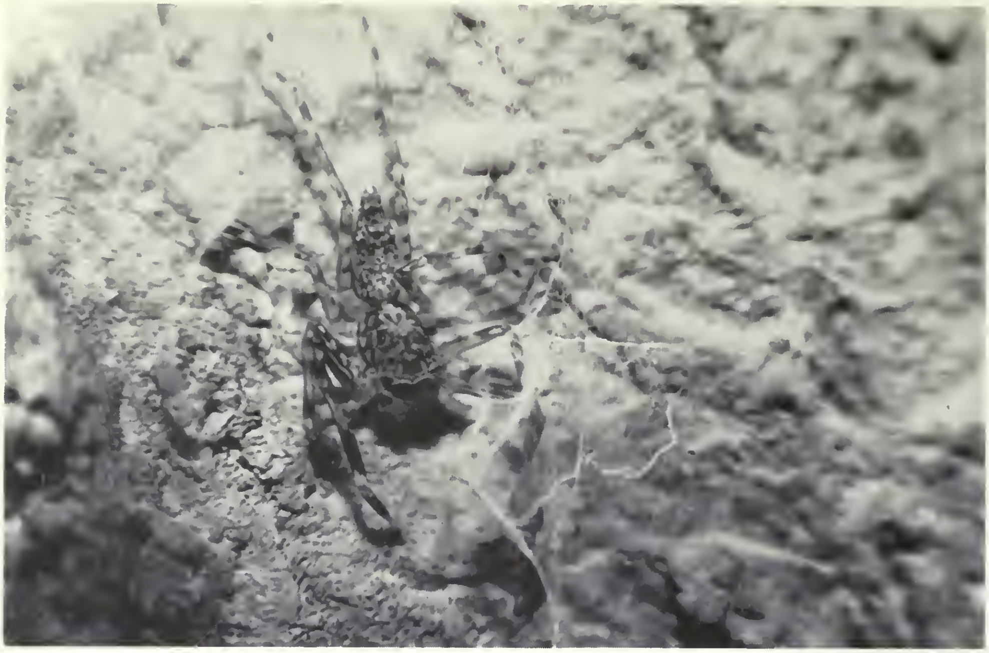

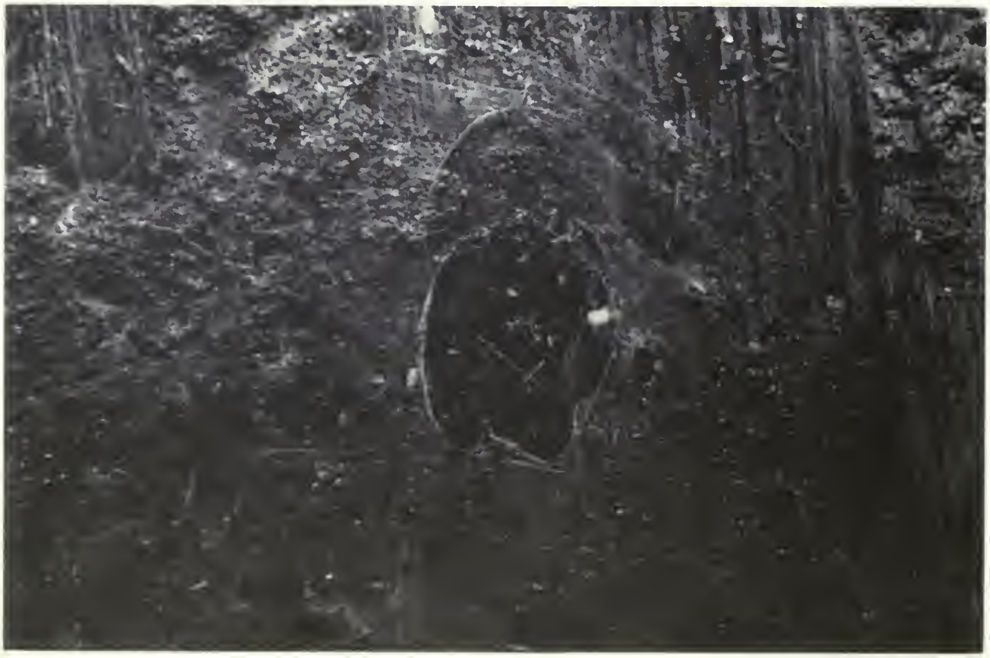

Fig. 1. (above) *Spartaeus wildtrackii* sp. n. Subadult ♂, under web on surface of tree trunk. **Fig. 2** (below) web of *Spartaeus wildtrackii* sp. n.

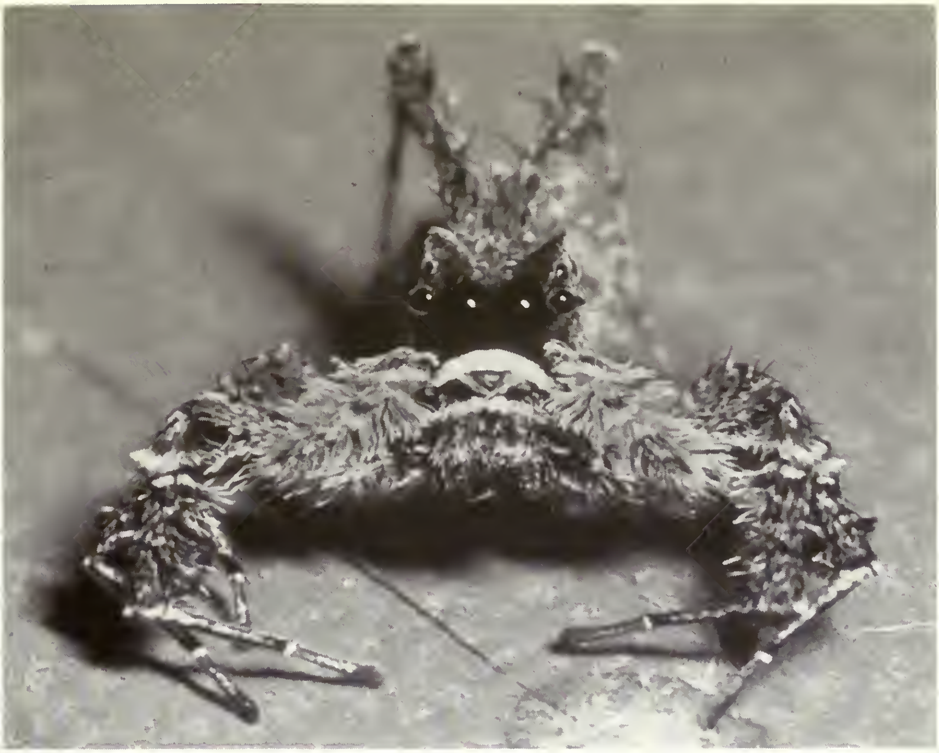

Fig. 3. *Portia labiata* (Thorell), ♀ from Malaysia.

1970 who noted that in *Cyrba algerina* (Lucas) pheromones left by the female stimulate the male and elicit searching behaviour.

Another feature clearly demonstrated by some of the species described below is the disparity in size of the posterior median eyes. In most spartaeines and also in a few other subfamilies the posterior median eyes are relatively large (Fig. 5A, B) and fully functional, whereas in most jumping spiders they are relatively small (Fig. 10A, B) with no demonstrable function. It is therefore of interest to note that in the species of *Taraxella* Wanless, described below there is a clear trend towards the development of small posterior median eyes. In practice the distinction between relatively large or relatively small becomes somewhat blurred in *Taraxella,* although there has hitherto been no difficulty in assigning one state or the other.

The presence of large posterior median eyes and web spinning behaviour in *Portia* species gave rise to the hypothesis (Jackson & Blest, 1982) that the ancestors of modern day salticids evolved from web building spiders with poorly developed vision and that acute vision, evolved originally in a spider like *Portia* that became an araneophagic predator, proficient at invading diverse types of webs. Subsequent papers on morphology (Wanless, 1984*a, b*) the evolution of salticid eyes (Blest, 1984; Blest & Sigmund, 1985) and behaviour (Jackson, 1985*b*; Jackson & Hallas, in press *a, b*) have given support to the hypothesis and suggest that although spartaeine salticids are highly specialized they may nevertheless represent one of the most primitive branches of the family.

Studies, however, are at an early stage for the biology of tropical salticids is very poorly known, in fact the majority of species cannot even be identified with confidence. Also, it is important to appreciate that the subfamily Spartaeinae, with more than 60 described species, represents less than 1·5% of the worlds salticid fauna. Despite this there are indications that jumping spiders make far more use of silk than has hitherto been supposed, for recent studies on other salticid groups have revealed species that build large prey-capture webs (Jackson, 1985*a*) and even species that live in groups forming nest complexes within the webs of other spiders (Jackson, in press).

The standard abbreviations and measurements are those made by Wanless (1978) but for the leg spination the system adopted is that used by Platnick & Shadab (1975). Note also, that the covering hairs on the male palps are not shown in any of the figures, because they are usually rather dense and obscure details.

Genus *SPARTAEUS* Thorell

Spartaeus: Wanless 1984*a*: 147 [synonymy, definition and species descriptions]. Blest & Sigmund, 1985: 129. Blest, 1985: 96.

Spartaeus is a small oriental genus comprising three species, *S. spinimanus* Thorell, from Indonesia, Malaysia and Sri Lanka, *S. thailandicus* Wanless from Thailand and *S. wildtrackii* sp. n., from Malaysia. They are easily distinguished by the structure of the genitalia.

All three species possess relatively large posterior median eyes (Fig. 4A), unusually long slender legs bearing numerous spines, and well developed femoral organs (Fig. 4E; 5E; 14A–C) on the first pair of legs of adult males. Also present on the legs of both males and females are disc-like mytiliform organs (Figs 15C; 16B). Those on the femora are more or less rounded and sparsely distributed (Fig. 16A), whereas those on the tibiae are ovoid and located distally on the dorsal surface of the segment (Fig. 15A, B). As mentioned above, mytiliform organs have hitherto only been found in the form of a patch on the dorsal surface of the abdomen. Their occurrence on legs is therefore of particular interest, especially as some are grouped on the distal end of the tibiae, an arrangement that may be unique to *Spartaeus*. However, at present these structures cannot be used to determine relationships as their distribution on the legs of other salticids is unknown. Furthermore, they are almost certainly homologous with pustuliform organs (see Hill, 1977 and Wanless, 1984) that occur as scattered pore-bearing pustules on the abdomen, legs and pedipalps of *Icius* Simon, *Metaphidippus* F.O.P-C and *Phidippus* Koch, and as a group on the abdomen of *Holcolaetis* Simon and *Sonoita* Peckham and Peckham.

The dorsal surface of the tibiae are characterised by hinge lines or rows of muscle attachment sites (Fig. 15A, B) that are electron dense and smooth in contrast to the surrounding cuticle. They resemble mytiliform organs, but lack pores and raised rims. It is also worth noting that they differ from the rows of triangular muscle attachment sites found on the tibiae and other leg segments of *Holcolaetis* species (see Wanless, 1985).

The biology of *Spartaeus* is unknown except for observations (see below) made by Mr P. D. Hillyard (BMNH) who also provided the photographs (Fig. 1; 2) showing *S. wildtrackii* beneath its sheet web on a tree trunk.

Spartaeus thailandicus Wanless
(Fig. 4A–I)

Spartaeus thailandica Wanless, 1984*a*: 151. Holotype ♀, Thailand, BMNH, [examined].

DIAGNOSIS. *S. thailandicus* seems to be most closely related to *S. wildtrackii* sp. n., but may be distinguished by the presence of a tegular apophysis (Fig. 4G, arrow) and the form of the retrolateral tibial apophysis (Fig. 4F) in males; females are separated by the absence of a postepigynal furrow (see Wanless 1984*a*, Fig. 5D).

MALE, in good condition, from Khas Yai National Park, Thailand. *Carapace* (Fig. 4A–D): weakly iridescent under some angles of illumination; orange-brown lightly tinged and mottled black with a broad tapering pale yellow band on thoracic part; rubbed except for some black and pale amber hairs on sides. *Eyes*: laterals with black surrounds; fringed by white hairs. *Clypeus*: yellow-brown with sooty markings; sparsely clothed in black and whitish hairs. *Chelicerae*: long robust and diverging; posterior surface with series of transverse furrows; orange-brown lightly tinged black; sparsely clothed in black hairs with dense promarginal scopula; fang robust and curved; fang groove with eight promarginal teeth and 12 retromarginal denticles. *Maxillae and labium*: pale brownish yellow faintly tinged with some black. *Sternum* (Fig. 4B): pale yellow-brown with darker margins. *Coxae*: pale yellow-brown except for blackish sides of I and II. *Abdomen*: pale yellow-brown with black markings, ventrally a broad sooty band from epigastric furrow to spinnerets;

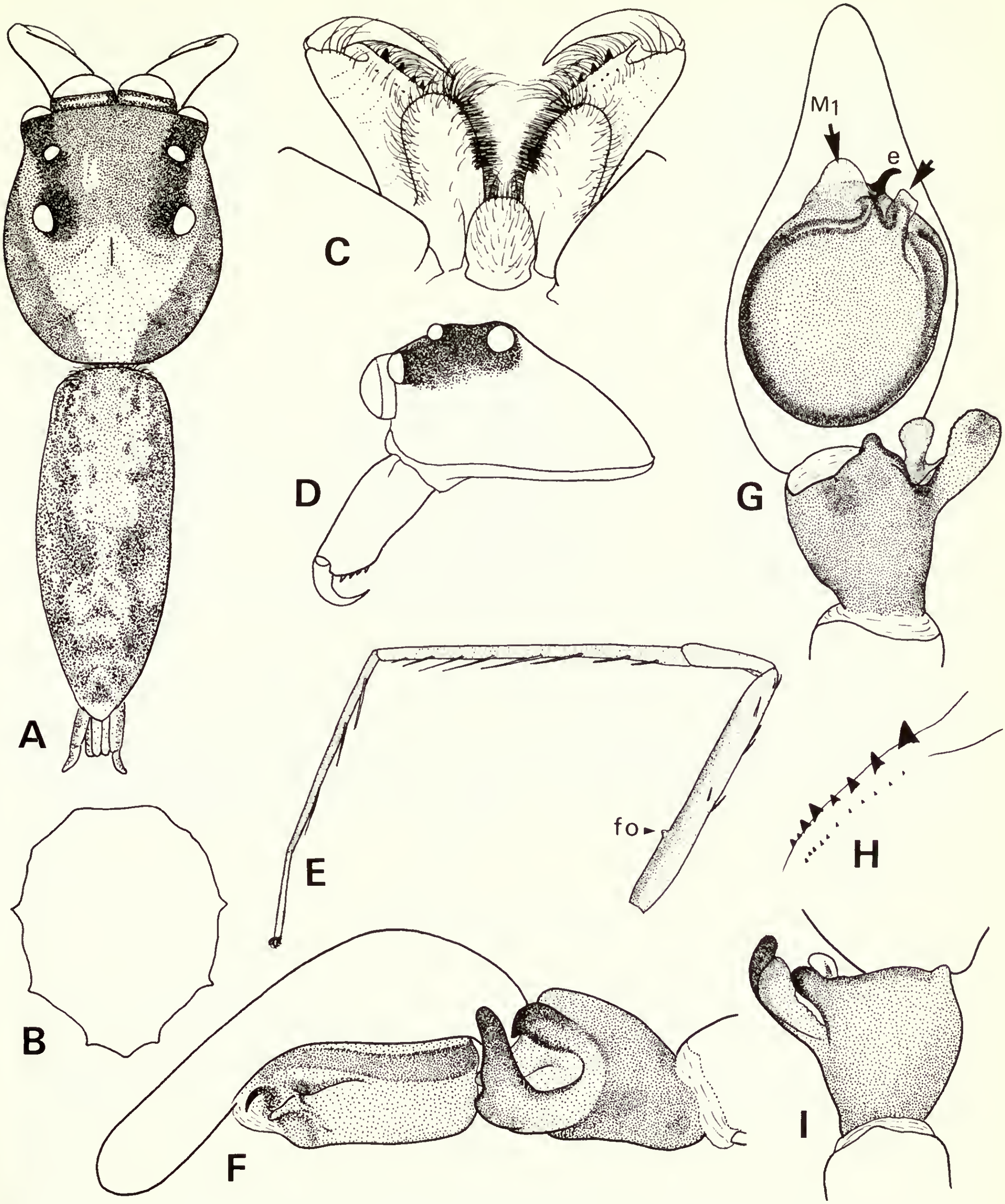

Fig. 4. *Spartaeus thailandicus* Wanless ♂, A, dorsal view; B, sternum; C, chelicerae, maxillae and labium; D, carapace, lateral view; E, leg I; F, palp, retrolateral view; G, palp, ventral view; H, cheliceral teeth; I, palpal tibia, dorsal view. Abbreviations: e, embolus; fo, femoral organ; M1, fan-shaped element of distal haematodocha.

rubbed; spinnerets long and robust. *Legs*: very long and slender, femoral organ pronounced; legs I yellow-brown except for blackish streaks on sides of femora, a blackish tinge towards apices of metatarsi and whitish yellow tarsi; other legs whitish yellow to yellow-brown with apices of metatarsi and tarsi tinged black; clothed in scattered simple and feathery hairs—mostly rubbed; tarsi I–II and apices of metatarsi I with proventral row of specialised prey-capture setae; metatarsi II–III with basal fringe of fine curved filamentous setae. Spines strong and numerous; spination of leg I: metatarsus v 2–4–0, tibia v 4–6–7, femur p 1–1–1, d 0–2–2, r 0–1–1. *Palp* (Fig. 4F, G, I): element M1 of the distal haematodocha (see Wanless, 1984*a*) fan-shaped (Fig. 4G); element M2 is obscure and appears to have fused with the base of the embolus.

Dimensions (mm): total length 8·5; carapace length 3·84, breadth 3·14, height 2·75; abdomen length 4·6; eyes, anterior row 2·7, middle row 2·04, posterior row 2·32; quadrangle length 1·9 (49% of carapace length).

Leg	1	2	3	4	Palp
Femur	6·40	3·84	3·56	4·56	1·60
Patella	2·60	1·72	1·44	1·60	0·88
Tibia	7·04	3·32	3·16	4·28	0·56
Metatarsus	5·36	3·16	3·64	5·28	——
Tarsus	1·96	1·14	1·16	1·36	1·68
Total	23·36	13·18	12·96	17·08	4·72

Ratios: AM : AL : PM : PL :: 22 : 13 : 8·5 : 12; AL—PM—PL : 12–14; AM : CL :: 22 : 5.

DISTRIBUTION. Thailand.

MATERIAL EXAMINED. **Thailand:** Khas Yai National Park, tropical evergreen forest, 1♂ under bark of decomposing log, 17.iii.1984, *P. D. Hillyard*, BMNH. 1985.8.16.1.

NATURAL HISTORY. The male described above was found together with several harvestmen (Opiliones) under the bark of a fallen decomposing log. There was no evidence of a web, but it was noticeable that the legs of this species were comparatively much longer than those of *S. wildtrackii*, a character that may enable future collectors to distinguish the species in the field.

Spartaeus wildtrackii sp. n.

(Figs 1; 2; 5A–E; 6A–D; 14A–C; 15A&C; 16A–D; 17A–G; 18A–D)

DIAGNOSIS. *S. wildtrackii* seems to be most closely related to *S. thailandica*, but may be distinguished by the absence of a tegular apophysis and the form of the retrolateral tibial apophysis in males (Fig. 6A, B, D), and the presence of a postepigynal furrow in females (Fig. 5D).

FEMALE HOLOTYPE, in fair condition. *Carapace* (Fig. 5A, B): weakly iridescent under some angles of illumination; orange-brown lightly tinged and mottled black with a broad yellow-brown tapering band on thoracic part and vague patches on sides; irregularly clothed in whitish hairs (mostly rubbed). *Eyes*: laterals with black surrounds; fringed by whitish and pale yellow hairs. *Clypeus*: sparsely clothed in black hairs. *Chelicerae*: robust, moderately long and more or less parallel; brownish orange lightly tinged black; thinly clothed in black hairs with dense promarginal scopula; promargin with six teeth, retromargin with nine or 12 denticles. *Maxillae and labium*: pale orange-brown lightly tinged with some grey. *Sternum*: pale yellow with darker margins. *Coxae*: pale yellow except first pair with blackish promarginal sides. *Abdomen*: pale yellow with blackish markings and scattered clumps of whitish guanin; ventrally a broad black band from epigyne to spinnerets; spinnerets long and robust. *Legs*: long and slender; legs I pale yellow to light orange-brown with vague sooty markings and a proventral black stripe on femora that appears iridescent green under

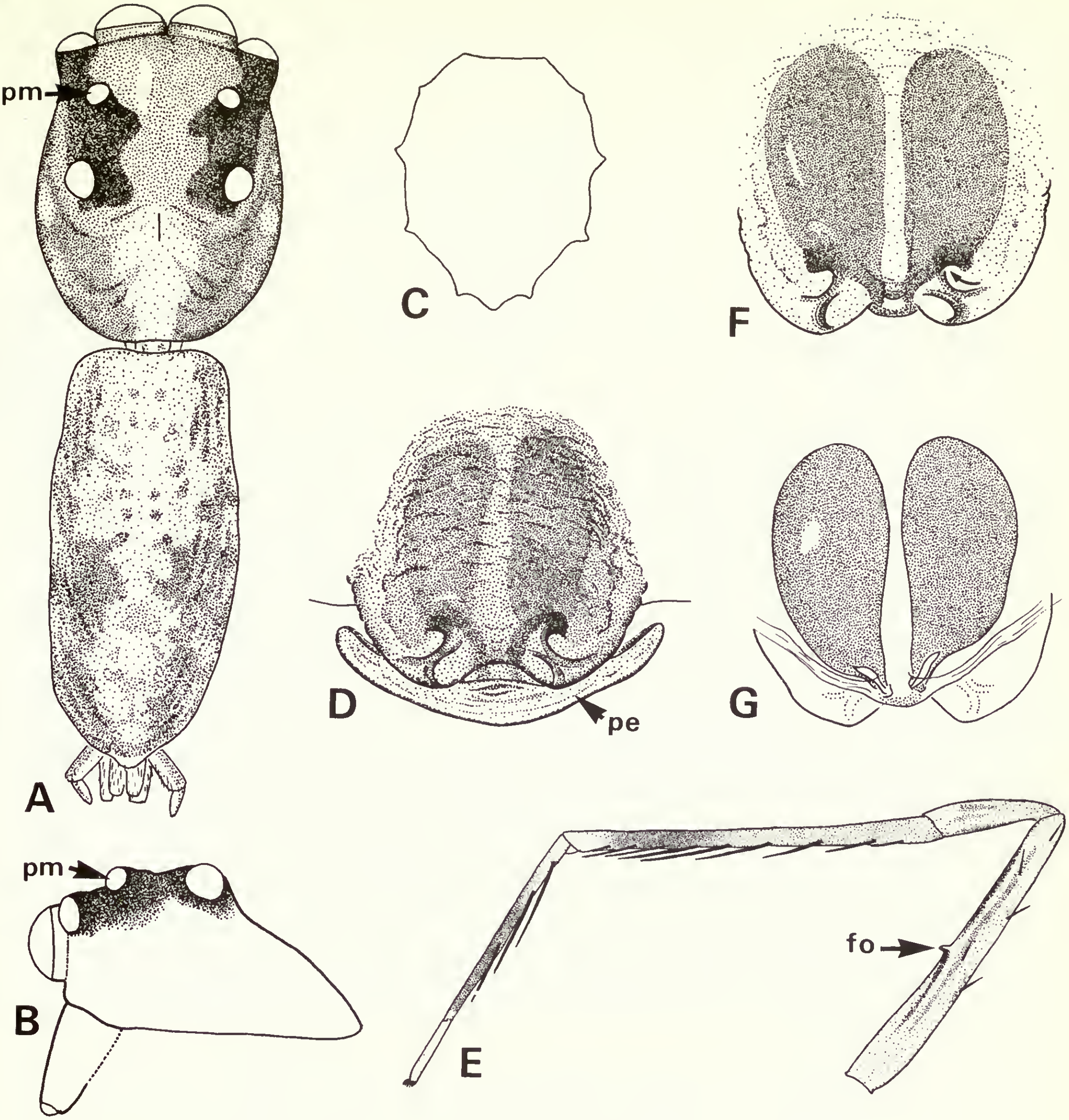

Fig. 5. *Spartaeus wildtrackii* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; D, epigyne. Paratype ♂: C, sternum; E, leg, I. Paratype ♀: F, vulva, ventral view; G, vulva, dorsal view. Abbreviations: pe, postepigynal furrow; pm, posterior median eye; fo, femoral organ.

some angles of illumination; other legs similar except femoral stripe lacking; also, dorsal spines arise from black spots; sparsely clothed in simple and feathery hairs, (Fig. 16D), mostly rubbed, with proventral row of specialized prey-capture setae on tarsi I–II (Fig. 17B, G) and apices of metatarsi I; proximal half of metatarsi II–III with scanty ventral fringe of fine curved filamentous setae (Fig. 17A, C–F). Spines strong and numerous; spination of leg I: metatarsus v 3–2–0, p 0–1–0, tibia v 5–8–7, femur d 0–2–1. *Palp*: with terminal claw; pale yellow with greyish patch on tarsus; clothed in pale yellow and light greyish hairs.

Dimensions (mm): total length 6·4; carapace length 2·72, breadth 2·28, height 1·52; abdomen length 3·68; eyes, anterior row 2·08, middle row 1·48, posterior row 1·75; quadrangle length 1·58 (58% of carapace length).

Leg	1	2	3	4	Palp
Femur	3·24	2·56	2·56	3·16	1·06
Patella	1·50	1·16	1·00	1·06	0·60
Tibia	3·16	2·20	2·20	3·04	0·64
Metatarsus	1·92	1·74	2·36	3·20	——
Tarsus	0·84	0·78	0·92	1·08	1·16
Total	10·66	8·44	9·04	11·54	3·46

Ratios: AM : AL : PM : PL :: 16·5 : 11 : 7 : 11; AL—PM—PL :: 10–10; AM : CL :: 16·5 : 3·5.

MALE PARATYPE, in good condition. *Carapace*: dark brown with dull orange-brown eye region and yellow-brown markings on thoracic part; clothed in fine recumbent light greyish and pale amber hairs. *Eyes*: laterals with black surrounds; fringed by pale yellow, whitish and amber hairs; also, a dense matt of short hairs behind anterior medians. *Clypeus*: tinged black, sparsely clothed in black hairs. *Chelicerae*: long, robust and slightly diverging; dark brown heavily tinged black; shiny; thinly clothed in black hairs with dense promarginal scopula; fang robust and curved with basal protuberance; promargin with eight teeth, retromargin with 12 (Fig. 6C). *Maxillae and labium*: orange-brown to yellow-brown tinged grey. *Sternum* (Fig. 5C): pale greenish yellow with darker margins; thinly clothed in greyish simple and feathery hairs. *Coxae*: pale greenish yellow with black promarginal stripe. *Abdomen*: yellow-brown suffused and mottled black; clothed in light and dark amber hairs with two spots comprised of whitish guanin; venter yellow-brown with grey-black band clothed in black feathery hairs from epigastric furrow to spinnerets; spinnerets long and robust. *Legs*: long and slender; femoral organ well developed (Fig. 5E; 14A–C); legs I pale greenish yellow to light orange brown with sooty markings and blackish longitudinal stripes on femora that shine iridescent green under some angles of illumination; thinly clothed in simple and black feathery hairs with some whitish ones on tarsi; specialized prey capture and filamentous hairs as in female. Spination of leg I: metatarsus v 3–1–1, p 0–0–1, r 1–0–0; tibia v 5–7–6; femur d 0–2–1, p 0–1–1. *Palp* (Fig. 6A, B, D): yellow-brown to light orange-brown with black iridescent stripe on underside of femora.

Dimensions (mm): total length 6·96; carapace length 3·36, breadth 2·68, height 1·92; abdomen length 3·8; eyes, anterior row 2·32, middle row 1·62, posterior row 1·96; quadrangle length 1·8 (54% of carapace length).

Leg	1	2	3	4	Palp
Femur	5·40	3·44	3·36	4·28	2·20
Patella	2·20	1·48	1·28	1·36	1·38
Tibia	5·68	3·16	3·08	4·20	1·08
Metatarsus	3·48	2·56	3·24	4·58	——
Tarsus	1·22	0·92	1·04	1·20	1·88
Total	17·98	11·56	12·00	15·62	6·54

Ratios: AM : AL: : PM : PL :: 19 : 11 : 8 : 11; AL—PM—PL :: 10 : 13; AM : CL :: 19 : 5.

VARIATION. Male total length varies from 6·24 to 7·44 mm, carapace length 2·72–3·36 mm (five specimens); female total length 6·0–6·96 mm, carapace length 2·56–3·36 mm (10 specimens).

In two females the arthrodial membrane between the chelicerae and the clypeus is evident as a narrow white band, whereas it is broad and conspicuous in other specimens. However, to judge from the set of the chelicerae it is apparent that the phenomenon is the result of postmorten changes.

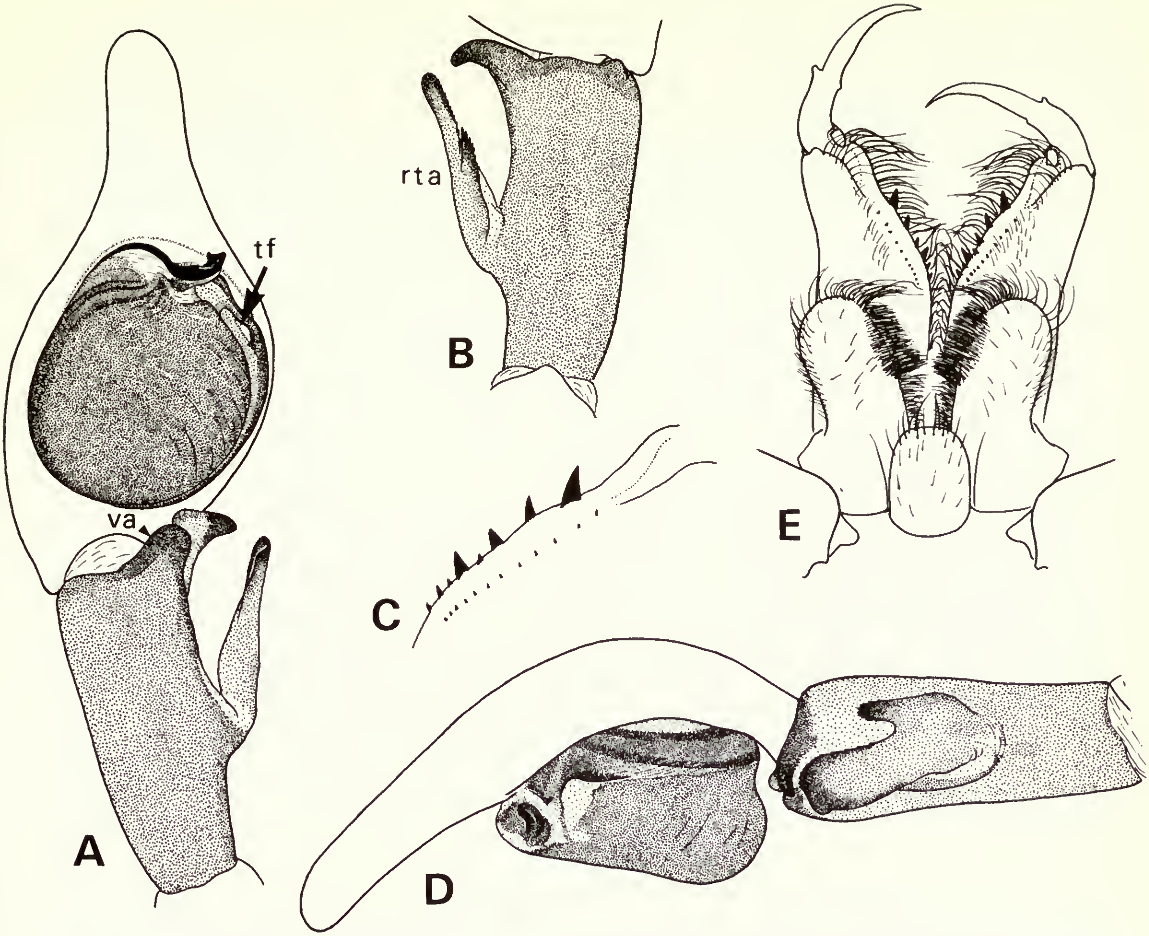

Fig. 6. *Spartaeus wildtrackii* sp. n., paratype ♂, A, palp, ventral view; B, palpal tibia, dorsal view; C, cheliceral teeth; D, palp, retrolateral view; E, chelicerae, maxillae and labium. Abbreviations: rta, retrolateral tibial apophysis, tf, tegular furrow; va, ventral apophysis.

NATURAL HISTORY. *S. wildtrackii* has so far only been found in lowland rainforest on the trunks of large trees covered in lichen or moss, against which the spiders are well camouflaged. A number of specimens were seen both at night and during the day resting on bark beneath large silken webs *ca.* 5–6 cm constructed of glossy translucent silk that was often torn (Fig. 1, 2). Their prey is unknown except for that of one specimen which was seen feeding on newly emerged moths, that were resting and evidently drying their wings. The spiders were not seen to jump, but it was noted that they were fast runners (P. D. Hillyard, pers. comm.).

DISTRIBUTION. West Malaysia.

MATERIAL EXAMINED. **West Malaysia,** *P. D. Hillyard*: Pahang State, Taman Negara, nr. Kuala Tahan, lowland primary rain forest: on tree trunks under sheet webs, 9.iii.1984, holotype ♀, BMNH. 1985.8.16.2, paratypes 3 ♀♀, BMNH. 1985.8.16.3–5; on tree trunks, iii.1985, paratypes 4 ♀♀, 4 ♂♂, BMNH 1985.8.16.6–13. Negeri Sembilan State, Pasoh Forest Reserve, on tree trunks in lowland primary rain forest, iii.1985, paratypes 3 ♂♂, 9 ♀♀, BMNH, 1985.8.16.14–25.

ETYMOLOGY. This species is named for the BBC television programme 'Wildtrack' which has done much to encourage children to care for the environment and take an interest in natural history.

REMARKS. 1. Postepigynal furrows (Fig. 5D) are an unusual feature of salticid epigynes and to date have only been found in one other spartaeine i.e. *Gelotia bimaculata* Thorell. Their function is uncertain, but they may form part of the supporting mechanism that holds the male palp in position during copulation.

2. Loerbroks (1984) has recently drawn attention to conspicuous similarities in palpal structure between *Misumena vatia* (Clerck), a crab spider (Family Thomisidae) and *Phaeacius* Koch, a genus of flattened salticid that has also been classified in the Spartaeinae. Futhermore, he has shown that in *M. vatia*, and probably all other thomisids, the ventral apophysis locks into the regular ridge as the palpal elements expand and rotate during copulation. The ventral apophysis (Figs 6A; 13F) and tegular furrow (Fig. 6A) (=tegular ridge of Loerbroks) characteristic of all spartaeines are evidently homologous with those of thomisids and probably function in a similar manner. In *M. vatia* the inner surface of the ventral apophysis is covered in papillae (see Loerbroks 1984, Fig. 6) that evidently reduce friction between the apophysis and the rotating tegulum. Similar papillae might therefore be expected on the ventral apophysis of *S. wildtrackii*, but are absent (Fig. 18A). However, spicule-like papillae do occur on the inner surface of the retrolateral tibial apophysis (Fig. 18B–D) and presumbly they too could reduce surface friction, although on the otherhand they may serve to prevent the apophysis from sliding out of position during copulaton.

Although genital structures are not generally used in assessing relationships at the familial level, they are considered here because ventral apophyses and tegular furrows are not known to occur in other spider families. They may have arisen independently, but as Loerbroks (1984) has already stated they may provide evidence of a phylogenetic link between salticids and thomisids. Additional evidence is provided by Homann (1971) who has shown that the anterior median eyes (principal eyes) of most spiders are small and have few visual cells, whereas those of salticids and thomisids are unique in possessing many visual cells which provide for 'sharp vision'. These optical similarities may be convergent as Homann regards thomisid eyes as being structurally closer to those of wolf spiders (Family Lycosidae). Future studies will have to take account of the genitalial similarities noted by Loerbroks since these can be interpreted as supportive of a sister group relationship between salticids and thomisids.

Genus *MINTONIA* Wanless

Mintonia Wanless, 1984*a*: 157. [definition, diagnosis and key to species].

This small oriental genus comprises nine species including two new taxa described below. The majority of species have been collected from Borneo, but the genus is also known from Java, Sumatra and Peninsular Malaya. Males are of particular interest because they possess femoral organs (Fig. 9D; 19A–C), a presumptive sex pheromone dispersal site, and retrolateral tibial apophyses, some of which bear openings (Fig. 9E arrowed; 20A, B). Unfortunately nothing is known of their natural history.

Mintonia melinauensis Wanless
(Fig. 7A–E)

Mintonia melinauensis Wanless, 1984*a*: 165, ♂ holotype, Sarawak (BMNH) [examined].

DIAGNOSIS. Males can be recognized by the heavy inward curving embolus and by the form of the retrolateral tibial apophysis (see Wanless, 1984*a*, Fig. 13); females by the structure of the epigyne (Fig. 7E) which is clearly different from that of other females of the genus.

FEMALE, formerly undescribed, in fair condition. *Carapace* (Fig. 7A, D): weakly iridescent under some angles of illumination; orange-brown lightly mottled black with paler lateral markings and band from fovea to posterior margin; rubbed, but otherwise clothed in whitish pubescent hairs. *Eyes*: laterals with black surrounds; fringed by whitish hairs. *Clypeus*: lightly tinged with some black; sparsely clothed in fine whitish hairs with several long bristles. *Chelicerae*: orange-brown suffused with some black proximally; shiny, thinly clothed in long pale orange hairs with moderately dense promarginal scopulae; promargin with three teeth, retromargin with six (Fig. 7B).

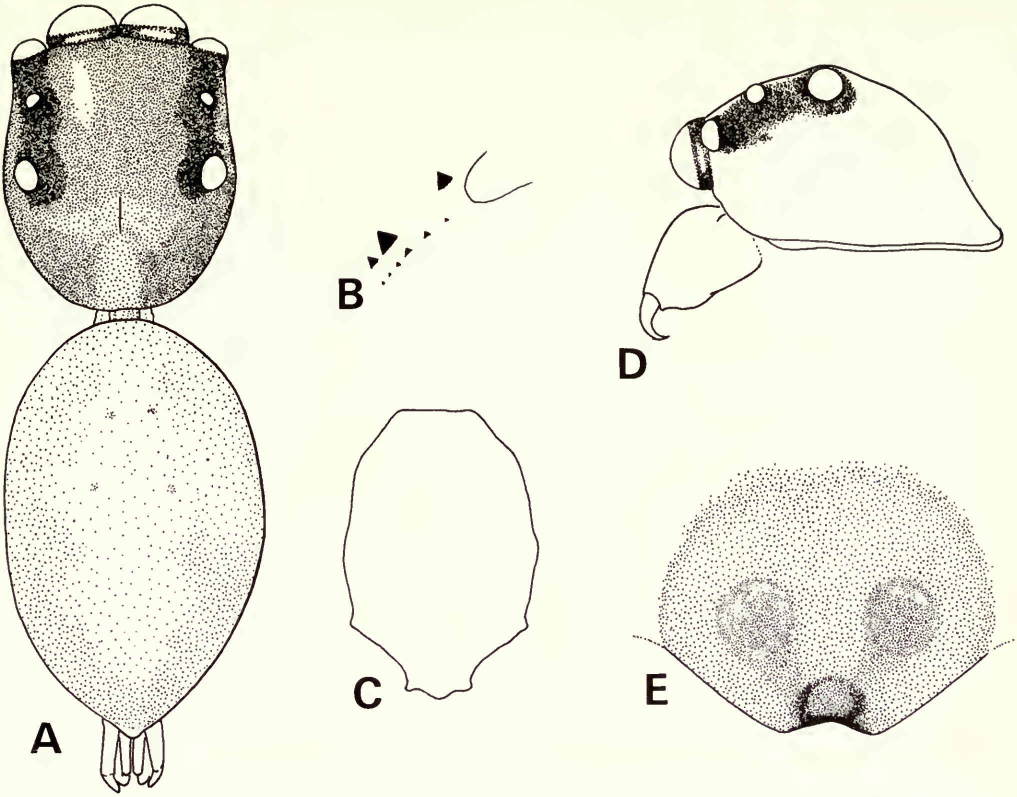

Fig. 7. *Mintonia melinauensis* Wanless, ♀: A, dorsal view; B, cheliceral teeth; C, sternum; D, carapace, lateral view; E, epigyne.

Maxillae: light orange-brown with whitish yellow inner distal margins. *Labium*: brownish orange tipped whitish yellow. *Sternum* (Fig. 7C): pale yellow with darker margins; thinly clothed in fine hairs. *Coxae*: pale greyish yellow. *Abdomen*: rubbed; whitish yellow with vague greyish markings; spinnerets whitish yellow with outer sides of anteriors tinged black. *Legs*: moderately long and robust; whitish yellow to orange brown; spines strong and numerous. Spination of leg I; metatarsus v 2–2–1, p 1–0–1, d 0–0–2, r 1–0–0; tibia v 2–2–2, p 1–0–1, r 0–0–1; patella p 0–1–0, r 0–1–0; femur d 0–2–3. *Palp*: whitish yellow with sooty markings except for pale orange brown tarsi. *Epigyne* (Fig. 7E): clothed in fine pale yellowish hairs.

Dimensions (mm): total length 5·2; carapace length 2·24, breadth 1·76, height 1·44; abdomen length 3·04; eyes, anterior row 1·64, middle row 1·48, posterior row 1·64; quadrangle length 1·2 (53% of carapace length).

Leg	1	2	3	4	Palp
Femur	1·48	1·46	1·48	1·80	0·80
Patella	0·86	0·81	0·71	0·76	0·48
Tibia	1·12	1·04	1·12	1·44	0·52
Metatarsus	0·96	0·94	1·16	1·60	——
Tarsus	0·58	0·57	0·60	0·68	0·72
Total	5·00	4·82	5·07	6·28	2·52

Ratios: AM : AL : PM : PL:: 13 : 8 : 5 : 8; AL—PM—PL :: 7·5–8·5; AM : CL :: 13 : 2·5.

Distribution. Sarawak.

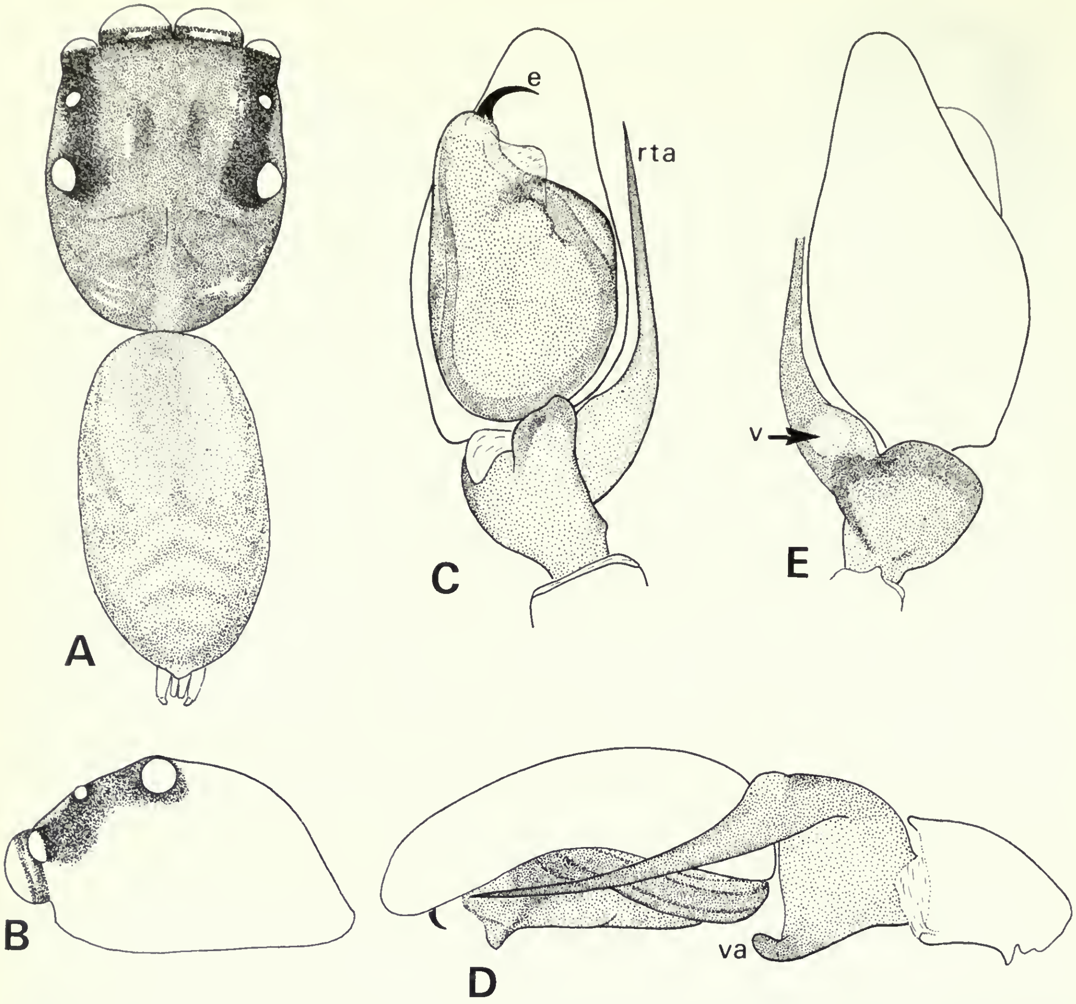

Fig. 8. *Mintonia caliginosa* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; C, palp, ventral view; D, palp, retrolateral view; E, palp, dorsal view. Abbreviations: e, embolus; rta, retrolateral tibial apophysis; v, vacuole; va, ventral apophysis.

Material examined. Type data given in synonymy. **Sarawak:** Gunung Mulu National Park, Environs of camp 3, moss forest, 1♀, from moss covered tree trunk, 27.5.78, *F. R. Wanless*, Royal Geographic Society/ Sarawak Government Expedition. (BMNH).

Mintonia caliginosa sp. n.
(Fig. 8A–E; 19A–C)

Diagnosis. A distinctive species easily recognized by the long retrolateral tibial apophysis (Fig. 8D).

Female. Unknown.

Male holotype, rubbed otherwise in fair condition. *Carapace* (Fig. 8A, B): orange-brown lightly tinged and mottled black; shiny and weakly iridescent under some angles of illumination. *Eyes*: laterals with black surrounds; fringed by whitish and pale amber hairs, mostly rubbed. *Clypeus* edged black below anterior median eyes; rubbed—a few whitish hairs remaining. *Chelicerae*: light brown with black markings, shiny, thinly clothed in scattered fine hairs; promargin with three teeth, retromargin with four or five. *Maxillae*: light yellowish brown. *Labium*: blackish edged pale yellow-brown. *Sternum*: yellow-brown, shiny, thinly clothed in fine greyish hairs. *Abdomen*: yellow-brown lightly tinged and mottled black with a poorly defined orange-brown scutum and chevrons dorsally, and three rather vague longitudinal bands ventrally; spinnerets yellow-brown lightly tinged black. *Legs*: moderately long and slender; femoral organ (Fig. 19A–C) a low tubercle; yellow-brown tinged with some black except metatarsi and tarsi which are darker—orange-brown tinged black, also on underside of femora I–II a transverse blackish patch; spines strong and numerous. Spination of leg I: metatarsus v 2–0–0, p 1–1–1, d 0–1–2, r 1–1–1; tibia v 2–2–2, p 1–1–0, d 1–1–0, r 1–1–0; patella p 0–1–0, r 0–1–0; femur d 0–2–4. *Palp* (Fig. 8C–E): the retrolateral tibial apophysis is broken at point arrowed in Fig. 8E; however, note that in Fig. 8C i.e. the same palp but drawn from a different angle, the appearance of the retrolateral tibial apophysis has been reconstructed from the apophysis of the other palp.

Dimensions (mm): total length 3·8; carapace length 1·76, breadth 1·36, height 1·1; abdomen length 1·92; eyes, anterior row 1·27, middle row 1·2, posterior row 1·35; quadrangle length 0·94 (53% of carapace length).

Leg	1	2	3	4	Palp
Femur	1·16	1·12	1·19	1·46	0·60
Patella	0·60	0·60	0·52	0·56	0·32
Tibia	0·84	0·80	0·88	1·16	0·24
Metatarsus	0·80	0·78	0·88	1·28	——
Tarsus	0·52	0·48	0·56	0·60	0·72
Total	3·90	3·78	4·03	5·06	1·88

Ratios: AM : AL : PM : PL :: 9·5 : 5·5 : 3·5 : 5·5; AL—PM—PL :: 6–7; AM : CL :: 9·5 : 3·3.

DISTRIBUTION. Borneo, Sabah.

MATERIAL EXAMINED. **Borneo:** Sabah, Tuaran Division, Mt. Kinabalu National Park, Power Station—Layang Layang, cloud forest, holotype ♂, 2000–2800 m, 7.ii.1976 *P. T. Lehtinen*, (TU, Turku).

REMARK. The presence of a vacuole in the base of the retrolateral tibial apophysis suggests that there is probably a distal opening. There is insufficient material for this to be confirmed by SEM.

ETYMOLOGY. The specific name is from the Latin meaning misty, cloudy places.

Mintonia silvicola sp. n.
(Fig. 9A–G)

DIAGNOSIS. *M. silvicola* seems to be most closely related to *M. tauricornis* Wanless, but may be readily distinguished by the syringe-shaped retrolateral tibial apophysis (Fig. 9E).

FEMALE. Unknown.

MALE HOLOTYPE, rubbed, also right leg I missing, otherwise in fair condition. *Carapace* (Fig. 9A, B): weakly iridescent under some angles of illumination; orange-brown with faint blackish mottling on sides. *Eyes*: laterals with black surrounds; anteriors fringed by whitish hairs. *Clypeus*: orange-brown with blackish margin below anterior median eyes and vague yellow-brown markings clothed in whitish hairs below anterior laterals. *Chelicerae*: yellow-brown, shiny, clothed in white hairs proximally and scattered brown hairs distally with dense promarginal scopulae; promargin with three teeth, retromargin with eight (Fig. 9G). *Maxillae*: yellow-brown with inner distal margins paler. *Labium*: yellow-brown faintly tinged grey. *Sternum*: pale yellow with vague darker margins; thinly clothed in fine pale yellow hairs. *Coxae*: pale yellow. *Abdomen*: pale yellow

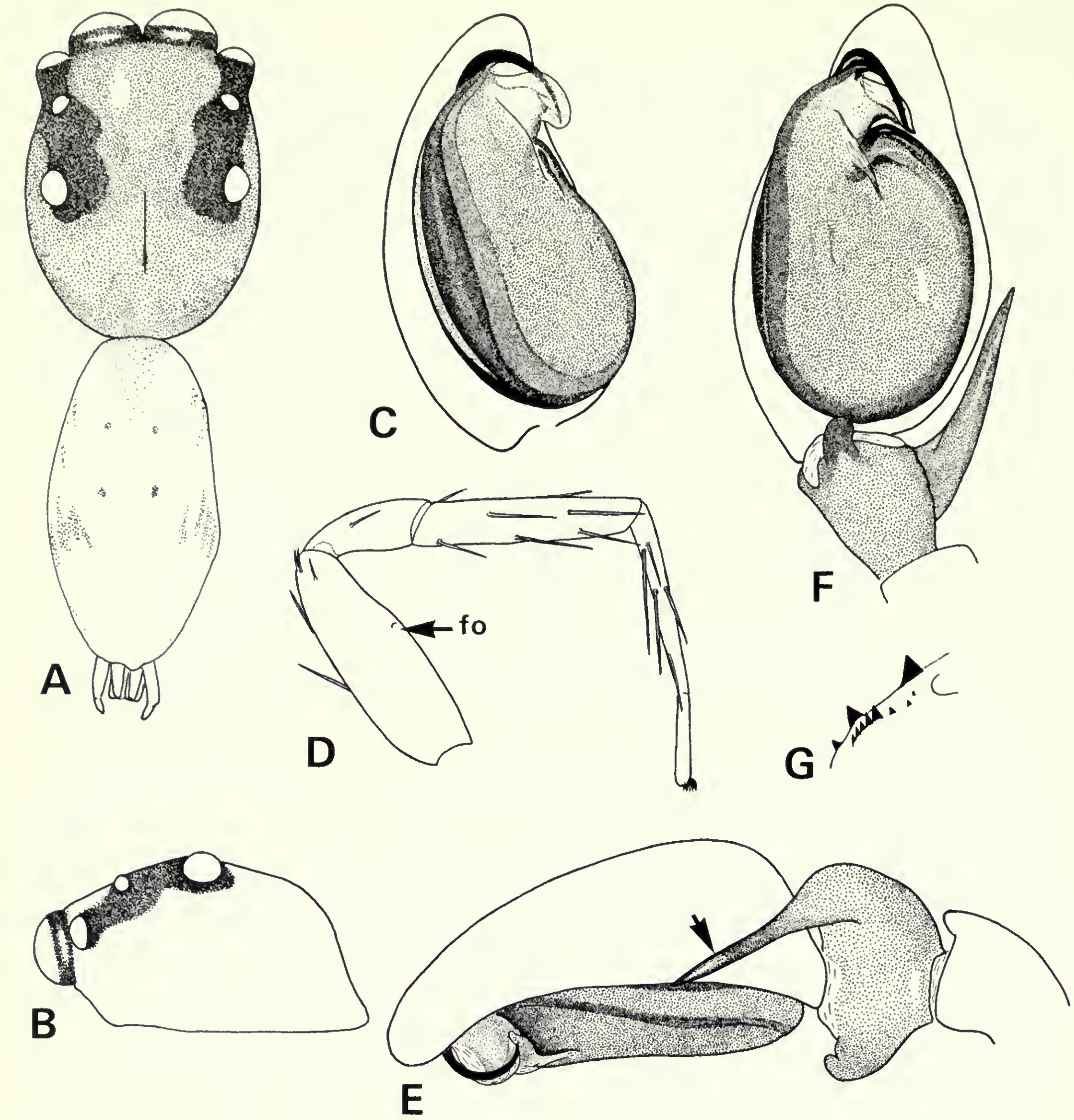

Fig. 9. *Mintonia silvicola* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; C, palp, ventrolateral view; D, leg I; E, palp, retrolateral view; F, palp, ventral view; G, cheliceral teeth. Abbreviation: fo, femoral organ.

with vague sooty markings and two pairs of sigilla; rubbed; spinnerets moderately long, yellow-brown. *Legs*: moderately long and slender; specialized prey capture and metatarsal setae lacking; femoral organ appearing as a low dark amber mound; legs I pale yellow to yellow-brown with underside of femora tinged black; other legs pale yellow grading to yellow-brown distally with ventral longitudinal grey stripe on tibiae II–III; spines numerous and moderately strong. Spination of leg I: metatarsus v 2–0–0, r 1–1–1, d 0–2–2, p 1–1–1; tibia v 2–2–2, p 1–1–0, d 1–1–0, r 1–1–0; patella p 0–1–0, r 0–1–0; femur d 0–2–4. *Palp* (Fig. 9C, E, F): element M2 lies above the embolus and the tegular ledge is poorly developed; the opening of the retrolateral tibial apophysis (arrow, Fig. 9E) is distinct.

Dimensions (mm): total length 5·1; carapace length 2·24, breadth 1·88, height 1·44; abdomen length 2·6; eyes, anterior row 1·71, middle row 1·48, posterior row 1·64; quadrangle length 1·32 (58% of carapace length).

Leg	1	2	3	4	Palp
Femur	1·72	1·72	1·72	2·04	0·84
Patella	0·88	0·84	0·76	0·80	0·40
Tibia	1·36	1·28	1·34	1·64	0·34
Metatarsus	1·28	1·26	1·44	1·80	——
Tarsus	0·64	0·64	0·72	0·76	1·12
Total	5·88	5·74	5·98	7·04	2·70

Ratios: AM : AL : PM : PL :: 14 : 8 : 5·4 : 8; AL—PM—PL :: 8–9·5; AM : CL :: 14 : 3.

DISTRIBUTION. West Malaysia.

MATERIAL EXAMINED. **West Malaysia**: Pahang State, Taman Negara, holotype ♂, from buttress of large tree, lowland rain forest nr. Kuala Tahan, 3–10.iii.1984. *P. D. Hillyard*, BMNH. 1985.8.21.1.

ETYMOLOGY. The specific name is from the Latin meaning inhabiting woods.

Genus ***TARAXELLA*** Wanless

Taraxella Wanless, 1984*a*: 155. [definition and diagnosis].

This genus was originally erected on the basis of a single male of *Taraxella solitaria* Wanless, from Sarawak. Subsequent collections have produced four new species, described below, that necessitate modifications to the original generic definition.

DEFINITION. Spiders small to medium in size, i.e. between 2·0 and 8·0 mm in length; males sometimes with conspicuous encircling band on the carapace; sexual dimorphism sometimes evident in colour patterns.

Carapace. high, longer than broad, widest at about level of coxae II–III; fovea long and sulciform, apex at level of centre of posterior lateral eyes. *Eyes*: anterior medians more or less level or weakly procurved in frontal view; posterior medians small to relatively large; posterior laterals with outer margins of lenses set inside or at level of, lateral margins of carapace when viewed from above; entire quadrangle length between 57–65% of carapace length. *Clypeus*: low to moderately high. *Chelicerae*: promargin with five or seven teeth, retromargin with seven or nine denticles. *Legs*: moderately long and slender; femoral organs lacking; specialized prey capture tarsal setae and filamentous metatarsal setae also lacking. *Female palps*: moderately long and slender with apical claw. *Epigynes*: interspecifically distinct, see descriptions; vulvae not examined, insufficient material. *Male palps*: complex and interspecifically distinct; retrolateral tibial apophyses complex, sometimes bifid with sharp slender prongs, or evidently reduced with associated stout setae; apophyses X and Y variable in development; embolus short slender and gently curved, and for the most part obscured, in ventral view, by tegular apophyses X and occasionally Y; tegular furrow and ventral apophysis usually conspicuous; M1, see Wanless 1984*a*, a delicate fan-shaped lamella that protrudes beyond the distal edge of the tegulum. Expanded palps not examined.

DIAGNOSIS. Distinguished from other spartaeines by the conformation of the embolus of the male palp which is almost completely obscured, in ventral view, by tegular apophyses 'X' and occasionally 'Y'.

An identification key is not provided as the five known species are easily separated from one another by the structure of the palpal organs and epigynes.

INTERSPECIFIC RELATIONSHIPS. To judge from the structure of the tibia of the male palpal organs *T. solitaria*, *T. petrensis* sp. n., and *T. hillyardi* sp. n., form a closely related group since they all possess retrolateral tibial apophyses with a sharp dorsal prong. *T. sumatrana* sp. n., and *T. reinholdae*

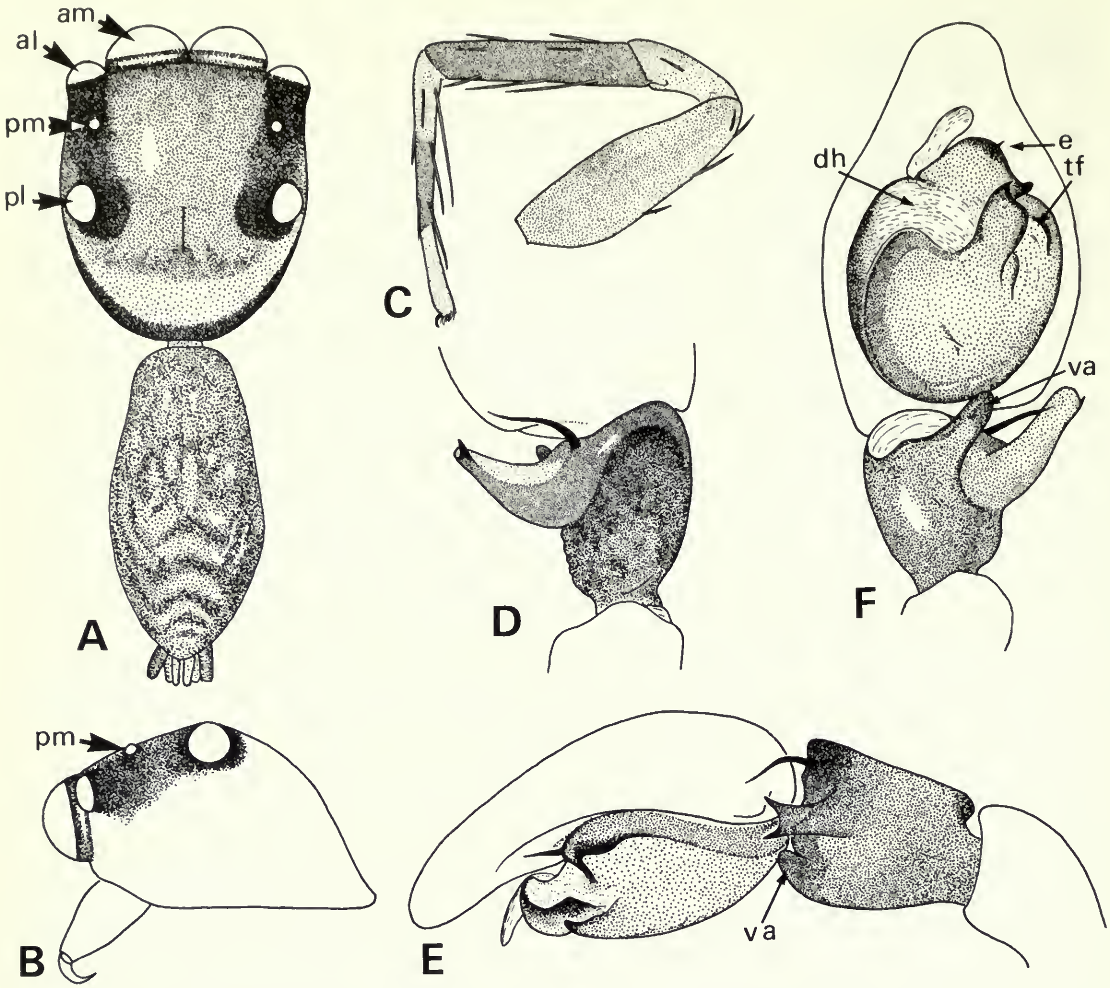

Fig. 10. *Taraxella hillyardi* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; C, leg I; D, palpal tibia, dorsal view; E, palp, retrolateral view; F, palp, ventral view. Abbreviations: al, anterior lateral eye; am, anterior median eye; dh, distal haematodocha; e, embolus; pl, posterior lateral eye; pm, posterior median eye; tf, tegular furrow; va, ventral apophysis.

would also appear to form a natural group as they possess conspicuous fringes of unusually stout setae, and lack retrolateral tibial apophyses with sharp dorsal prongs.

Taraxella hillyardi sp. n.
(Fig. 10A, F)

DIAGNOSIS. *T. hillyardi* seems to be most closely related to *T. petrensis* and *T. solitaria,* but can be easily distinguished by the bifid retrolateral tibial apophysis (Fig. 10E).

FEMALE. Unknown.

MALE HOLOTYPE, in fair condition. *Carapace* (Fig. 10A, B): weakly iridescent under some angles of illumination; light orange-brown tinged black with a broad yellowish encircling band on sides and also a black marginal band extending posteriorly from level of coxae I; rubbed. *Eyes*: laterals with black surrounds; sparsely fringed in pale amber and whitish hairs. *Clypeus*: greyish with black markings below anterior median eyes and whitish yellow stripes below anterior laterals; sparsely fringed by whitish hairs. *Chelicerae*: yellow-brown with extensive patches on facies; shiny; thinly clothed in fine clear hairs and some blackish ones with dense promarginal scopulae; promargin with five teeth; retromargin with eight denticles. *Maxillae and labium*: pale yellow with vague sooty markings. *Coxae*: yellow-brown. *Abdomen*: dorsum and sides pale yellow-brown suffused and mottled black, venter pale yellow brown suffused black in region of tracheal spiracle; spinnerets moderately long; anteriors and posteriors suffused black, medians pale yellow. *Legs* Fig. 10C): moderately long and slender; generally yellow-brown tinged with some black, with incomplete annuli on femora and blackish tibiae particularly of legs I and IV; spines moderately strong and numerous. Spination of leg I: metatarsus v 2–0–0, p. 1–1–1, d 0–2–2, r 1–1–1; tibia v 2–2–2, p 0–1–1, d 1–1–0, r 1–1–0; patella p 0–1–1, r 0–1–0; femur d 0–2–3, p 0–0–1. *Palp* (Fig. 10D–F): yellow-brown to orange-brown mottled black with patches of white hairs on patella and apices of femur, otherwise clothed in black hairs and scattered white ones with greyish scopula on cymbium.

Dimensions (mm): total length 3·9; carapace length 1·76, breadth 1·53, height 1.2; abdomen length 1·84; eyes, anterior row 1·56, middle row 1·24, posterior row 1·52; quadrangle length 1·07 (60% of carapace length).

Leg	1	2	3	4	Palp
Femur	1·36	1·28	1·28	1·64	0·68
Patella	0·76	0·63	0·56	0·64	0·33
Tibia	1·12	0·96	1·00	1·39	0·36
Metatarsus	1·02	0·96	1·12	1·60	——
Tarsus	0·53	0·52	0·56	0·66	0·72
Total	4·79	4·35	4·52	5·93	2·09

Ratios: AM : AL : PM : PL :: 13 : 7 : 3 : 7; AL—PM—PL :: 7–8; AM : CL :: 13 : 3.

DISTRIBUTION. West Malaysia.

MATERIAL EXAMINED. **West Malaysia**: Gunong Jerai, (Kedeh), ca. 700 m, holotype ♂, shrub layer, along forest edge during middle of dry season, 15.ii.1983, *P. D. Hillyard* (BMNH. 1985.9.5.2).

ETYMOLOGY. This species is named after my colleague Mr P. D. Hillyard, BMNH, who collected many of the new species described in this paper.

Taraxella petrensis sp. n.
(Fig. 11A–J)

DIAGNOSIS. *T. petrensis* seems to be most closely related to *T. solitarius* and *T. hillyardi* sp. n., but may be easily separated by the broad flange of the retrolateral tibial apophysis (Fig. 11J) in males and the structure of the epigyne (Fig. 11D) in females.

MALE HOLOTYPE, rubbed otherwise in good condition. *Carapace* (Fig. 11A, F): shiny and weakly iridescent in eye region; dark orange-brown suffused black with broad encircling creamy white band. *Eyes*: laterals with black surrounds; anteriors sparsely fringed in greyish hairs. *Clypeus*: creamy white with black spots near lower rims of anterior median eyes. *Chelicerae*: shiny black except for orange-brown inner margins; sparsely clothed in greyish hairs with dense promarginal scopulae; promargin with five teeth, retromargin with nine denticles (Fig. 11C). *Maxillae and labium*: greyish yellow faintly tinged black. *Sternum*: pale yellow-brown with darker margins; thinly clothed in light brownish hairs. *Coxae*: yellow-brown tinged grey. *Abdomen*: yellow-brown with dorsum and sides mottled black, also a vague black patch in area of tracheal slit; rubbed; spinnerets moderately long, black except for light greyish medians. *Legs*: moderately long and slender; yellow-brown heavily suffused black, especially on femora, patellae and tibiae; shiny and

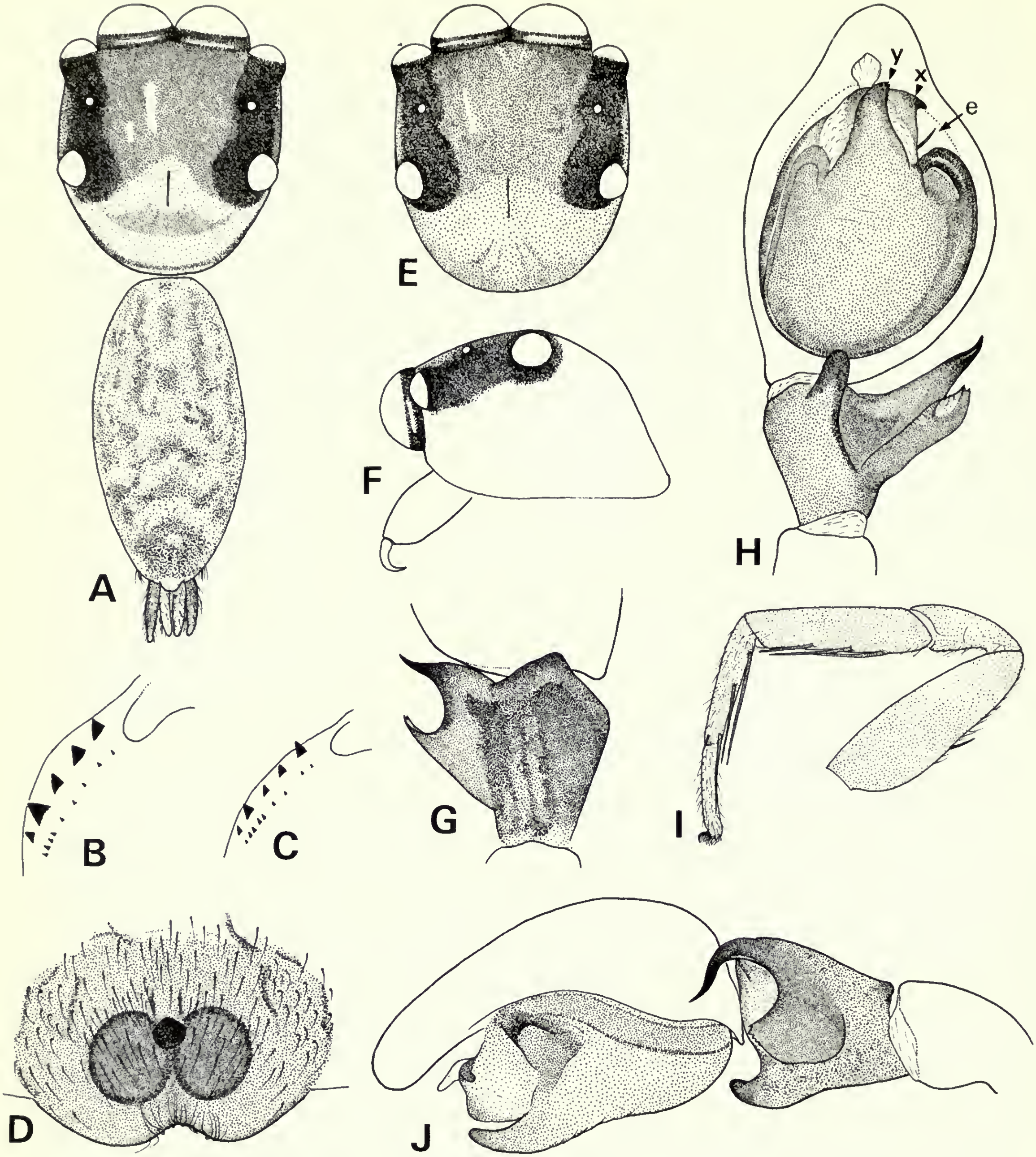

Fig. 11. *Taraxella petrensis* sp. n., holotype ♂: A, dorsal view; C, cheliceral teeth; F, carapace, lateral view; G, palpal tibia, dorsal view; H, palp, ventral view; J, palp, retrolateral view. Paratype ♂: B, cheliceral teeth; E, carapace, dorsal view; I, leg I. Abbreviation: e, embolus; 'x' and 'y' tegular apophyses.

iridescent under some angles or illumination; spines strong and numerous. Spination of leg I: metatarsus v 2–2–2, p 1–0–0, d 0–1–2, r 1–0–0; tibia v 1–3–2, p 0–1–1, d 1–1–0, r 0–0–1; patella p 0–1–0, r 0–1–0; femur d 0–2–3. *Palp* (Fig. 11G, H, J): yellow to orange-brown suffused with some black especially on femur and cymbium; clothed in pale grey and black hairs.

Dimensions (mm): total length 3·72; carapace length 1·76, breadth 1·56, height 1·24; abdomen length 2·16; eyes, anterior row 1·6; middle row 1·21, posterior row 1·52; quadrangle length 1·08 (61% of carapace length).

Leg	1	2	3	4	Palp
Femur	1·52	1·34	1·36	1·72	0·76
Patella	0·76	0·60	0·60	0·66	0·32
Tibia	1·24	1·00	1·04	1·42	0·36
Metatarsus	1·12	1·02	1·18	1·65	——
Tarsus	0·60	0·56	0·56	0·70	0·84
Total	5·24	4·52	4·74	6·15	2·28

Ratios: AM : AL : PM : PL :: 13·5 : 7·5 : 2·5 : 7·5; AL—PM—PL :: 7·5 : 7; AM : CL :: 13·5 : 5.

FEMALE PARATYPE, in fair condition. General habitus as in male except encircling cephalic band lacking. *Carapace* (Fig. 11E): light orange-brown lightly and finely reticulated black in eye region with blackish mottling on sides, also weakly iridescent under some angles of illumination; rubbed. *Eyes:* generally as in male, but sparsely fringed by pale amber hairs. *Clypeus*: light orange-brown faintly reticulated black; bald except for scattered fine marginal hairs and several long stiff hairs including usual triad in lower space between anterior median eyes. *Chelicerae*: yellow-brown lightly tinged with some black; shiny; sparsely clothed in brown hairs with dense promarginal scopulae; promargin with five teeth, retromargin with nine denticles (Fig. 11B). *Maxillae and labium*: yellow-brown. *Sternum*: pale yellow-brown with darker margins; sparsely clothed in fine hairs centrally and darker, longer ones towards margins. *Abdomen*: generally as in male except venter pale yellow-brown with scattered dark brown simple hairs and vague light greyish feathery hairs, otherwise rubbed; spinnerets similar to male, yellow-brown tinged black. *Legs* (Fig. 11I): moderately long and slender; light orange-brown faintly tinged with some black; sparsely clothed in brownish hairs; spines strong and numerous. Spination of leg I: metatarsus v 2–2–0, p 1–0–1, d 0–1–2, r 0–0–1; tibia v 2–3–1, p 0–1–1; patella p 0–1–0; femur d 0–2–2. *Epigyne* (Fig. 11D).

Dimensions (mm): total length 4·32; carapace length 1·96, breadth 1·72, height 1·32; abdomen length 2·28; eyes, anterior row 1·76, middle row 1·36, posterior row 1·72; quadrangle length 1·2 (61% of carapace length).

Leg	1	2	3	4	Palp
Femur	1·58	1·44	1·44	1·76	0·76
Patella	0·84	0·74	0·64	0·70	0·43
Tibia	1·18	1·00	1·08	1·46	0·48
Metatarsus	1·04	1·00	1·20	1·68	——
Tarsus	0·60	0·56	0·63	0·64	0·67
Total	5·24	4·74	4·99	6·24	2·34

Ratios: AM : AL : PM : PL :: 15 : 8 : 2 : 8; AL—PM—PL :: 8–9; AM : CL :: 15 : 2.

DISTRIBUTION. West Sumatra.

MATERIAL EXAMINED. **West Sumatra:** Harau Nature Reserve, near Payakumbu, holotype ♂, on rock walls on edge of forest, ca. 600 m, ii.1985, *P. D. Hillyard,* (BMNH. 1985.9.5.1); Taram, near Payakumbu, in secondary forest litter, paratype ♀, ii.1985, *P. D. Hillyard,* (BMNH. 1985.9.5.2).

ETYMOLOGY. The specific name is from the Latin meaning rocky places.

Taraxella sumatrana sp. n.
(Fig. 12A–J)

DIAGNOSIS. Easily separated from other species of *Taraxella* by the dorsal fringe of stout setae on the palpal tibia (Fig. 12G, J) in males and by the structure of the epigyne in females (Fig. 12D).

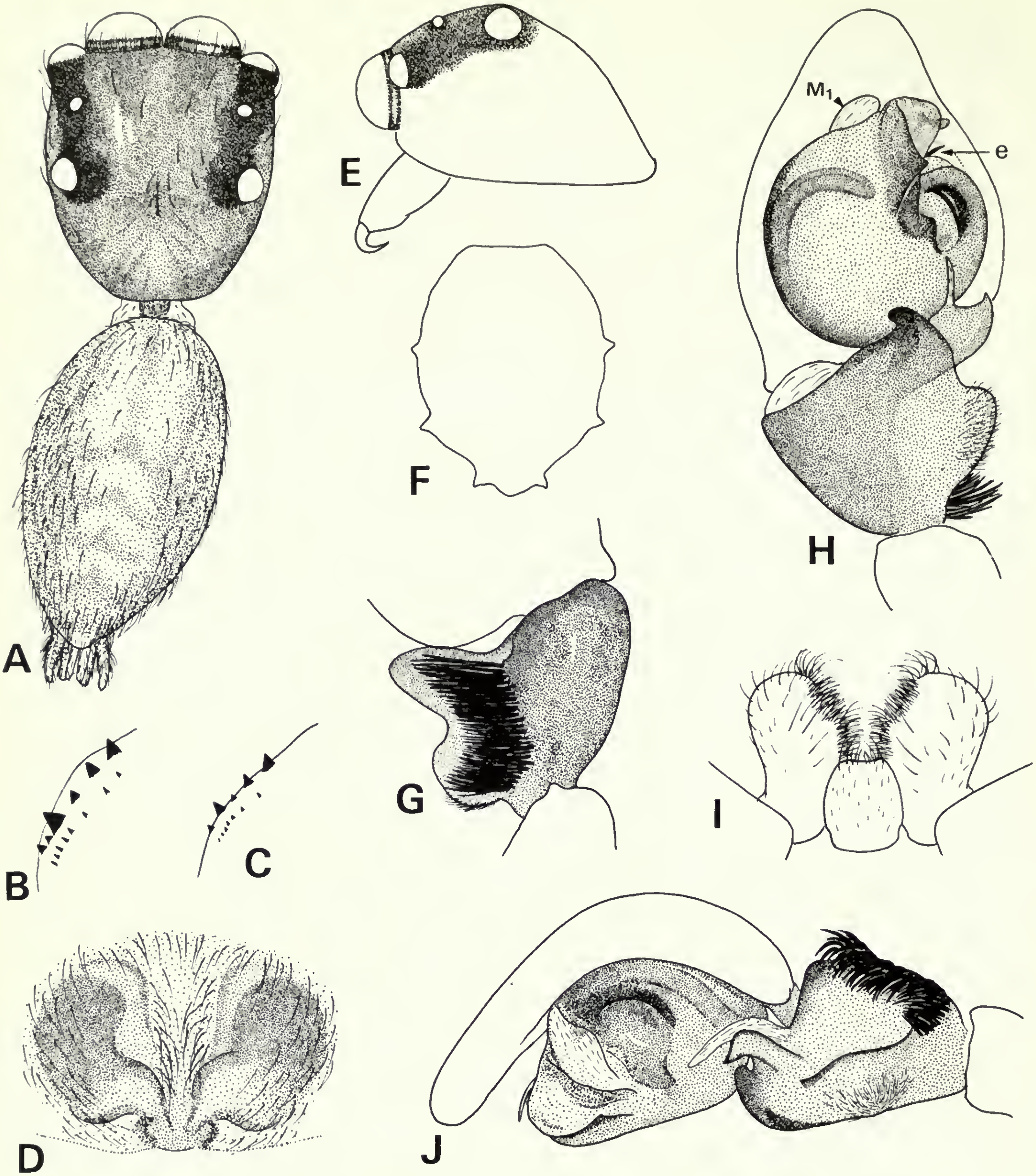

Fig. 12 *Taraxella sumatrana* sp. n., holotype ♀: A, dorsal view. B, cheliceral teeth; D, epigyne; F, sternum; I, maxillae and labium. Paratype ♂: C, cheliceral teeth; E, carapace, lateral view; G, palpal tibia, dorsal view; H, palp, ventral view; J, palp, retrolateral view. Abbreviations: e, embolus; M1, fan-shaped element of distal haematodocha.

Female holotype, in fair condition. *Carapace* (Fig. 12A): yellow-brown faintly tinged and mottled black with a metallic sheen under some angles of illumination; rubbed except for some scattered brown hairs. *Eyes*: laterals with black surrounds; fringed by light brownish hairs and some whitish ones below anterior median eyes. *Clypeus* yellow-brown tinged black with a few black bristles. *Chelicerae*: pale yellow-brown, shiny, sparsely clothed in brown-black hairs and some bristles with dense promarginal scopulae; promargin with six teeth, retromargin with eight denticles (Fig. 12B). *Maxillae and labium*: pale yellow-brown. *Sternum* (Fig. 12F): pale yellow-brown with darker margins; thinly clothed in stiff brown hairs. *Coxae*: pale yellow-brown. *Abdomen*: pale yellow-brown tinged and mottled black with vague chevrons dorsally; venter pale greyish yellow; mostly rubbed otherwise sparsely clothed in patches of recumbent dull amber lanceolate hairs, thinly interspersed with erect black hairs; spinnerets moderately long, pale yellow brown except anteriors tinged with some black. *Legs*: moderately long and slender; generally pale yellow-brown faintly tinged with some black; thinly clothed in pale greyish and black hairs; spines moderately strong and numerous. Spination of leg I: metatarsus v 2–0–0, r 0–1–1, d 0–1–2, p 1–1–1; tibia v 1–3–2, p 0–1–1; patella p 0–1–0; femur d 0–2–3. *Epigyne* (Fig. 12D): clothed in dark grey hairs.

Dimensions (mm): total length 4·44; carapace length 2·0, breadth 1·68, height 1·32; abdomen length 2·32; eyes, anterior row 1·72, middle row 1·38, posterior row 1·61; quadrangle length 1·12 (56% of carapace length).

Leg	1	2	3	4	Palp
Femur	1·52	1·36	1·36	1·76	0·76
Patella	0·78	0·68	0·62	0·68	0·40
Tibia	1·12	0·96	1·00	1·40	0·52
Metatarsus	1·02	0·96	1·11	1·56	——
Tarsus	0·56	0·56	0·58	0·70	0·66
Total	5·00	4·52	4·67	6·10	2·34

Ratios: AM : AL : PM : PL :: 14 : 8 : 4 : 8; AL—PM—PL :: 7–7·5; AM : CL :: 14 : 3.

MALE PARATYPE, abdomen and legs IV missing, otherwise in fair condition. Similar to female except for the following. *Carapace* (Fig. 12E): heavily suffused and mottled black especially on sides; rubbed except for shining violet hairs behind anterior eyes. *Clypeus*: with scattered fine whitish hairs. *Chelicerae*: yellow-brown with sooty markings, shiny, clothed in scattered black hairs with dense promarginal scopulae; promargin with five teeth retromargin with seven denticles (Fig. 12C). Spination of leg I: metatarsus v 2–2–2, r 1–0–0, d 0–2–2, p 1–0–0; tibia v 1–3–2, p 0–1–1, r 1–0–1, d 1–0–0; patella p 0–1–0, r 0–1–0; femur d 0–2–3. *Palp* (Fig. 12G, H, J): femur and patella pale yellowish lightly suffused black; tibia and cymbium light to dark amber mottled with some black; clothed in brownish hairs with patch of white hairs on patella and apices of femora.

Dimensions (mm): total length ?; carapace length 1·92, breadth 1·22, height 1·32; abdomen length ?; eyes, anterior row 1·64, middle row 1·29, posterior row 1·52; quadrangle length 1·12 (58% of carapace length).

Leg	1	2	3	4	Palp
Femur	1·58	1·44	1·40	——	0·80
Patella	0·76	0·68	0·60	——	0·36
Tibia	1·26	1·04	1·08	——	0·46
Metatarsus	1·16	1·08	1·22	——	——
Tarsus	0·62	0·60	0·64	——	0·92
Total	5·38	4·84	4·94	——	2·54

Ratios: AM : AL : PM : PL :: 14 : 8 : 4 : 8; AL—PM—PL :: 6–7; AM : CL :: 14 : 5.

DISTRIBUTION. Sumatra.

MATERIAL EXAMINED. **Sumatra**, Bohorok, Gunung Leuser Reserve: holotype ♀, in litter, 14.vi. 1983, *P. R. Deeleman* and *C. L. Deeleman-Reinhold*; paratype ♂, in bamboo litter on plateau with large bamboo trees, 50 m, 10.ii.1983, *P. R. Deeleman* and *S. Djojosudharma* (Rijksmuseum van Natuurlijke Histoire, Leiden).

ETYMOLOGY. The specific name refers to the country in which the holotype was collected.

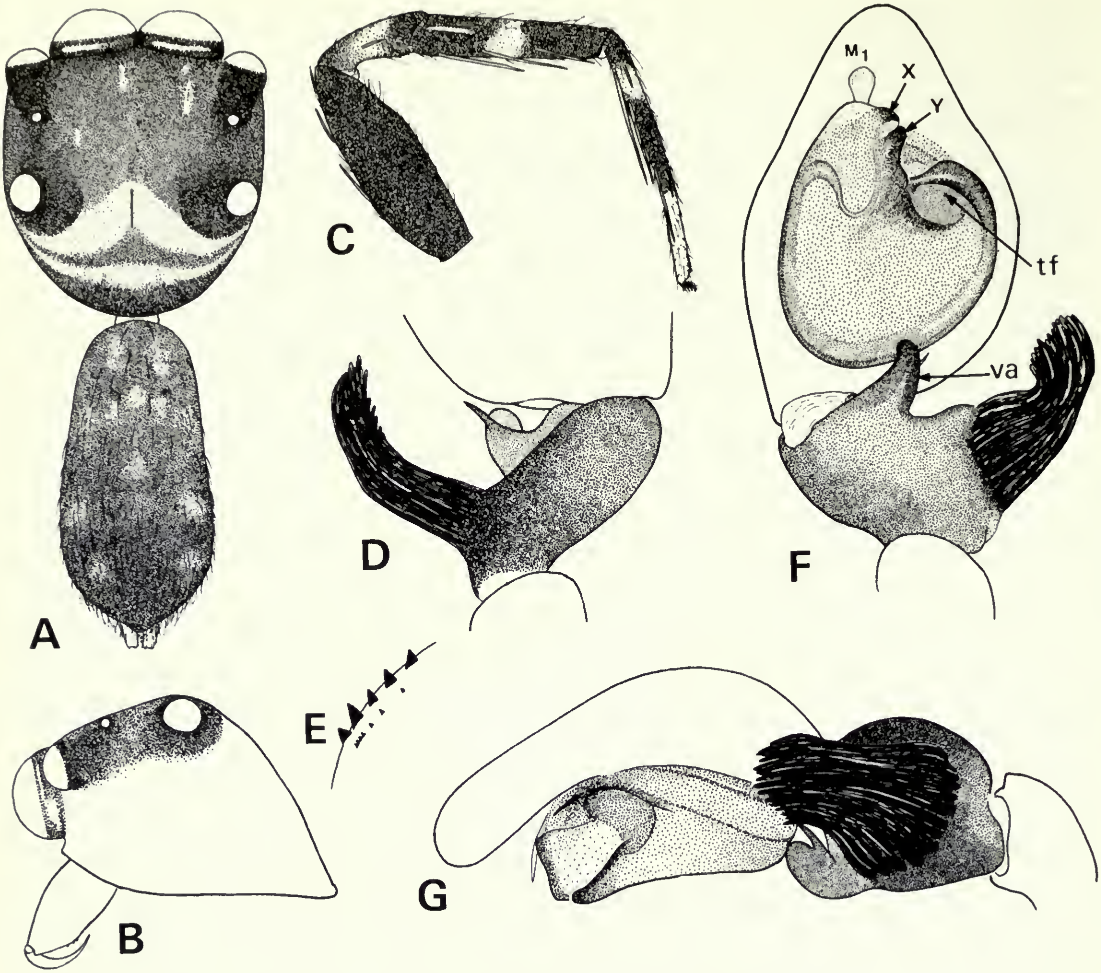

Fig. 13. *Taraxella reinholdae* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; C, leg I; D, palpal tibia, dorsal view; E, cheliceral teeth; F, palp, ventral view; G, palp, retrolateral view. Abbreviations: M1, fan-shaped element of distal haematodocha; tf, tegular furrow; va, ventral apophysis; 'x' and 'y', tegular apophyses.

Taraxella reinholdae sp. n.
(Fig. 13A–G)

DIAGNOSIS. Easily separated from other species of *Taraxella* by the conspicuous tuft of stout setae arising from the retrolateral surface of the palpal tibial apophysis (Fig. 13D, F, G).

FEMALE. Unknown.

MALE HOLOTYPE in fair condition. *Carapace* (Fig. 13A, B): mottled black with metallic sheen and pale yellowish green markings on thoracic part; irregularly clothed, in scattered black and white hairs with a central white haired stripe behind anterior median eyes. *Eyes*: laterals with black surrounds; fringed by white hairs with scattered dark grey hairs around laterals and upper rims of anterior medians. *Clypeus*: clothed in scattered white hairs. *Chelicerae*: black with metallic sheen except for light greyish amber inner margins; sparsely clothed in light greyish hairs with moderately dense promarginal scopulae; promargin with five teeth, retromargin with seven denticles (Fig. 13E). *Maxillae and labium*: pale yellow-brown heavily mottled black with whitish inner distal margins on maxillae and labial tip. *Sternum*: yellow-brown suffused black; shiny, with scattered fine blackish hairs. *Coxae*: pale greyish yellow suffused with some black. *Abdomen*: dorsum and sides yellowish green heavily tinged black; clothed in brown-black hairs with vague patches of whitish hairs laterally; venter pale yellow with black surrounds, clothed in grey black hairs; spinnerets black with blackish hairs. *Legs* (Fig. 13C): moderately long and slender; generally black except for pale yellowish brown tarsi and yellow-brown annuli on metatarsi, tibiae and patellae; spines strong and numerous. Spination of leg I: metatarsus v 2–0–0, p 1–0–2, d 1–1–2; tibia v 2–2–2, p 1–0–1, d 1–1–0; patella p 0–1–0, r 0–1–0; femur d 0–2–3. *Palp* (Fig. 13D, F, G): patella pale yellow tinged with some black, other segments heavily mottled black; clothed in black hairs with patch of whitish hairs on patella and apices of femora.

Dimensions (mm): total length ca. 3·2 (bent); carapace length 1·52, breadth 1·44, height 1·16; abdomen length 1·68; eyes, anterior row 1·48, middle row 1·16, posterior row 1·40; quadrangle length 1·0 (65% of carapace length).

Leg	1	2	3	4	Palp
Femur	1·28	1·18	1·20	1·56	0·64
Patella	0·66	0·58	0·54	0·60	0·32
Tibia	1·02	0·84	0·88	1·20	0·32
Metatarsus	0·96	0·88	0·96	1·42	——
Tarsus	0·52	0·48	0·52	0·61	0·72
Total	4·44	3·96	4·10	5·39	2·00

Ratios: AM : AL : PM : PL :: 7 : 12·5 : 2 : 7; AL—PM—PL :: 8–7; AM : CL :: 12·5 : 3·5.

DISTRIBUTION. Borneo, Sarawak.

MATERIAL EXAMINED. **Sarawak:** Bako National Park, holotype ♂, in litter, in swampy forest, 29–30.iii.1985. *C. L. Deeleman-Reinhold* and *P. R. Deeleman,* (RNH, Leiden).

ETYMOLOGY. This species is named for one of the collectors Dr C. L. Deeleman-Reinhold.

Acknowledgements

I would like to thank Dr C. L. Deeleman-Reinhold, Ossendrecht, Holland and Dr P. Lehtinen, University of Turku, Turku, Finland for allowing me to study their collections of oriental salticids.

I am also indebted to my colleague Mr P. D. Hillyard for collecting spiders in Indonesia and Malaysia and for providing photographs for Figs 1–2. Mrs F. Murphy, London kindly supplied the photograph for Figure 3.

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—— **&** —— (in press *b*). Predatory versatility and intraspecific interactions of spartaeine jumping spiders (Araneae: Salticidae): *Brettus adonis, B. cingulatus, Cyrba algerina*, and *Phaeacius* sp. n. *N.Z. Jl. Zool.*

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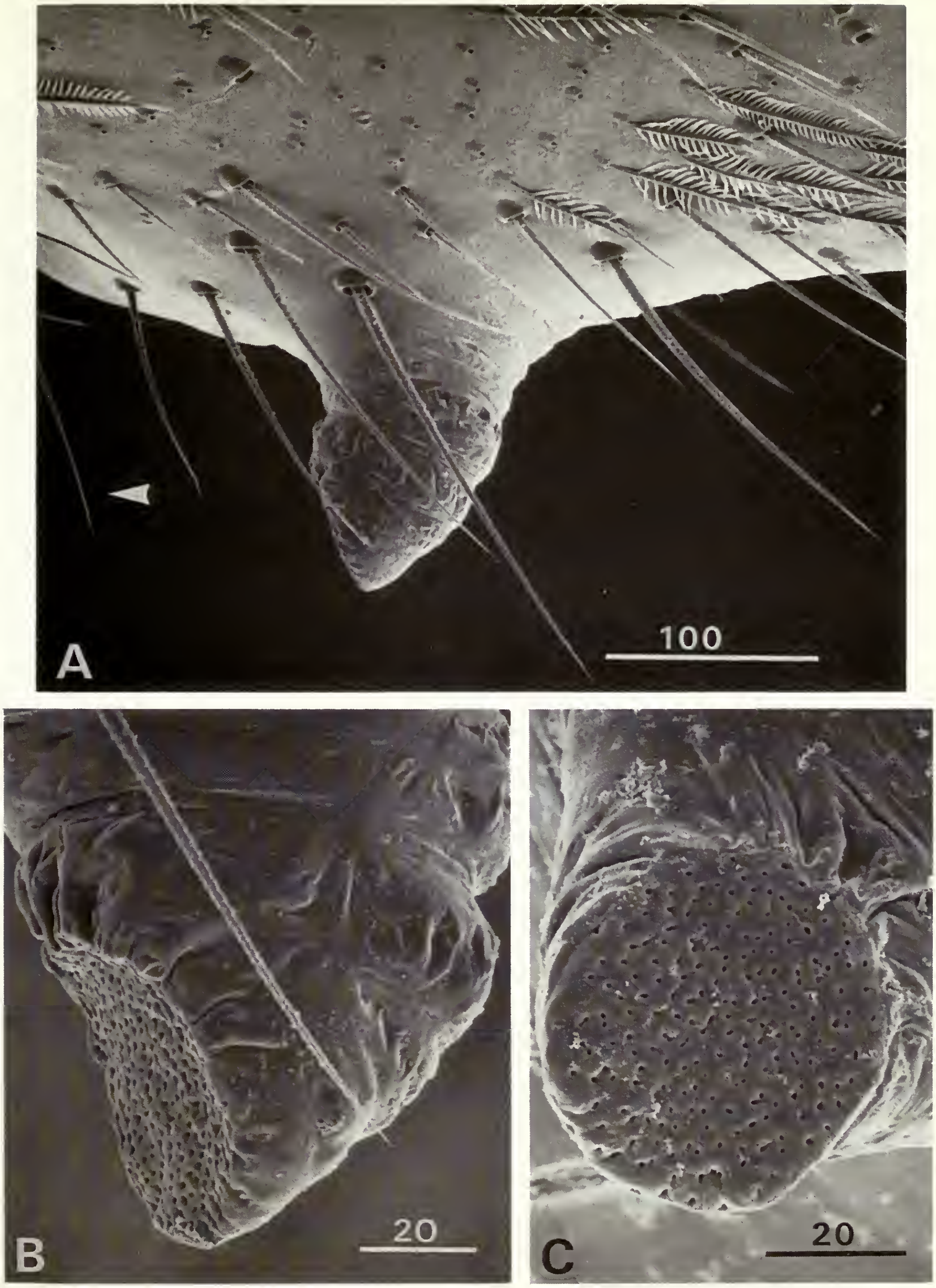

Fig. 14. *Spartaeus wildtrackii* sp. n., paratype ♂: femoral organ: A, × 316; B, × 820; C, × 1040. Scale bars μm. Arrow indicates direction of coxa.

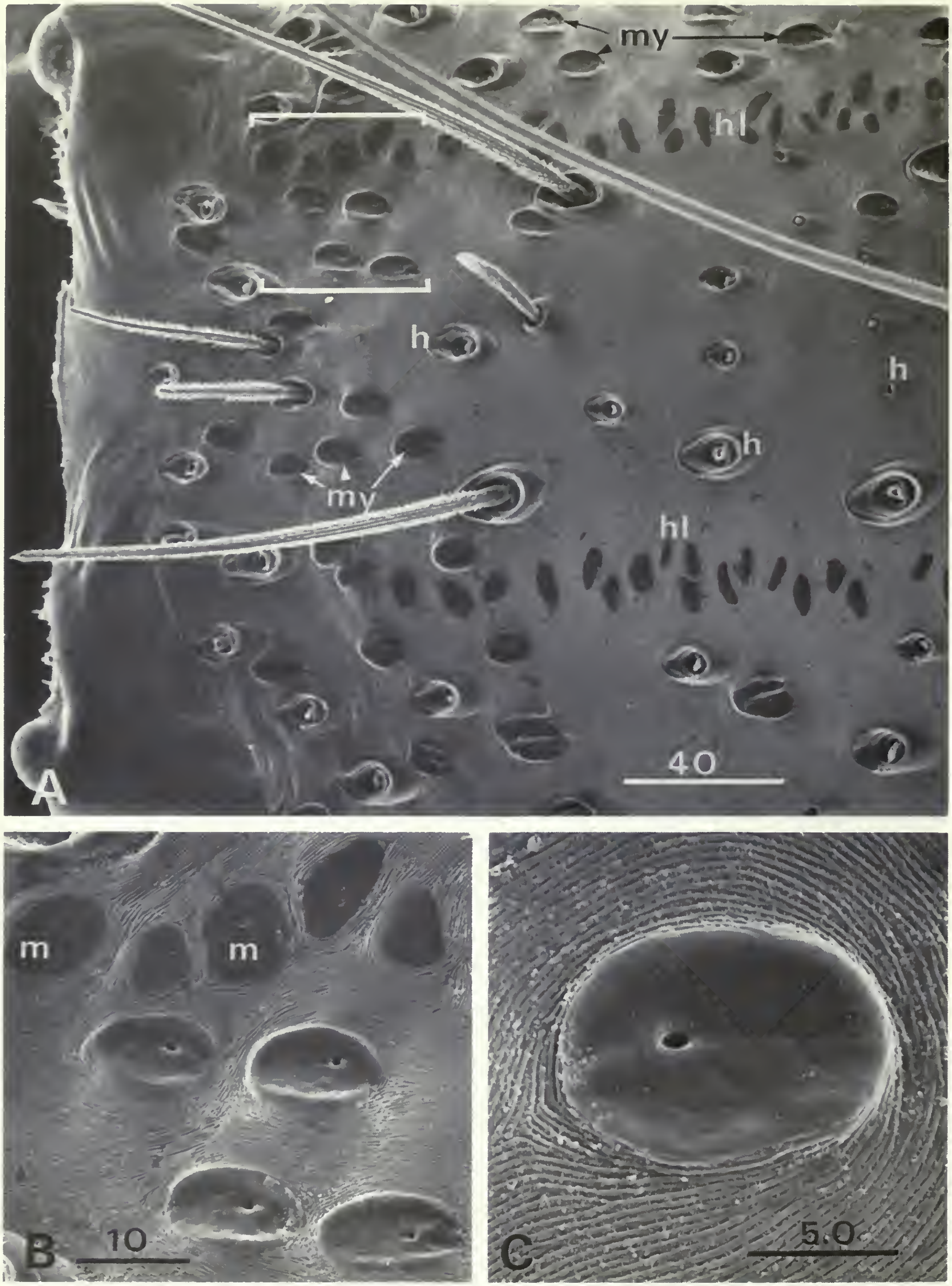

Fig. 15. *Spartaeus wildtrackii* sp. n., ♂, tibia II: A, dorsal view of distal region showing distribution of mytiliform organs and muscle attachment sites, × 570; B, mytiliform organs and muscle attachment sites, × 1600; C, detail of mytiliform organ, × 4200. Abbreviations: h, hair sockets; hl, hinge line; m, muscle attachment site; my, mytiliform organ. Scale bars µm.

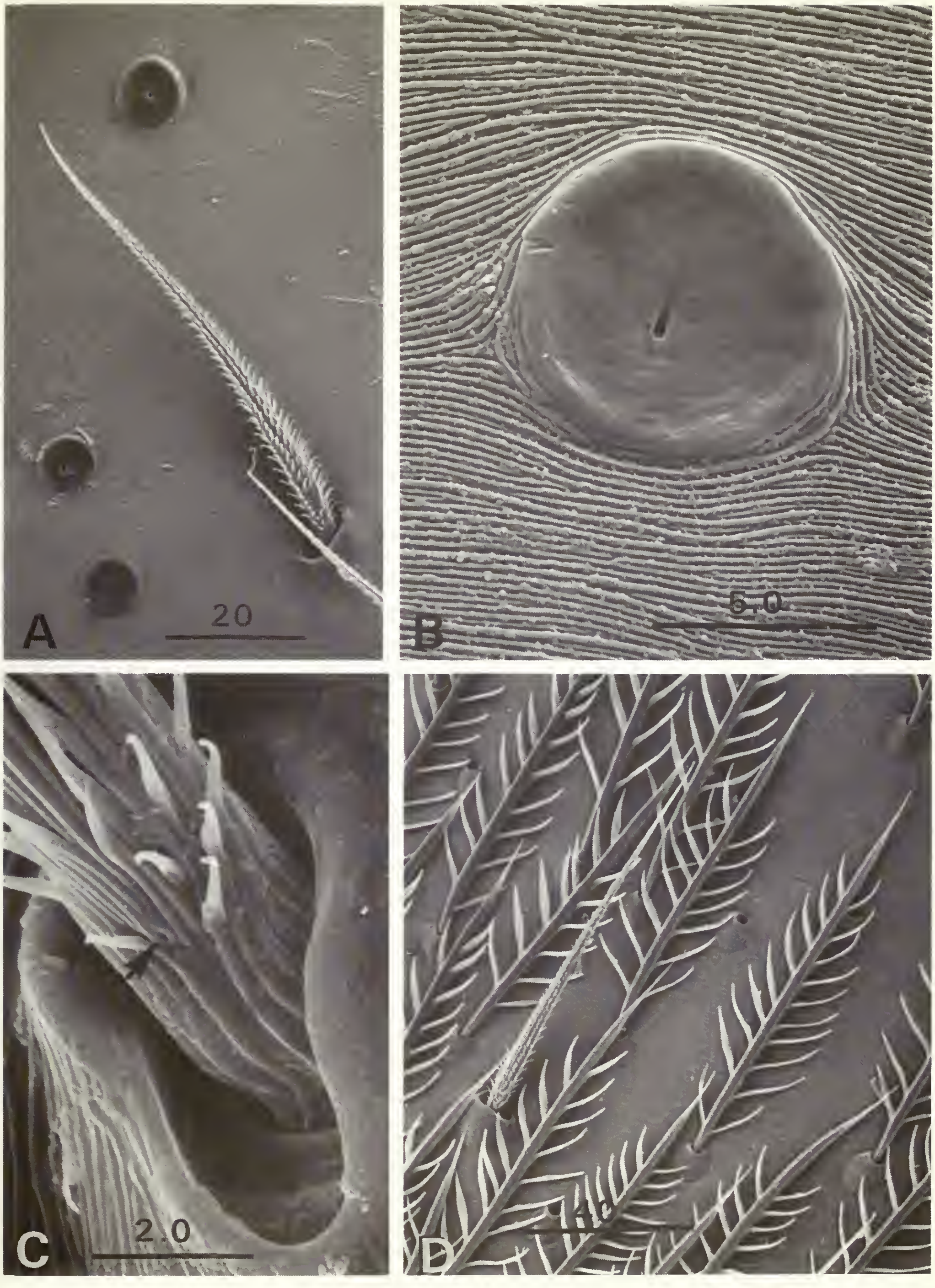

Fig. 16. *Spartaeus wildtrackii* sp. n., ♂: A, femora I, mytiliform organs and seta, × 1000; B, femora II, detail of mytiliform organ, × 6200; C, metatarsus II, base of filimentous seta showing dendritic pore, × 10300; D, femora I, feathery setae, × 620. Scale bars μm.

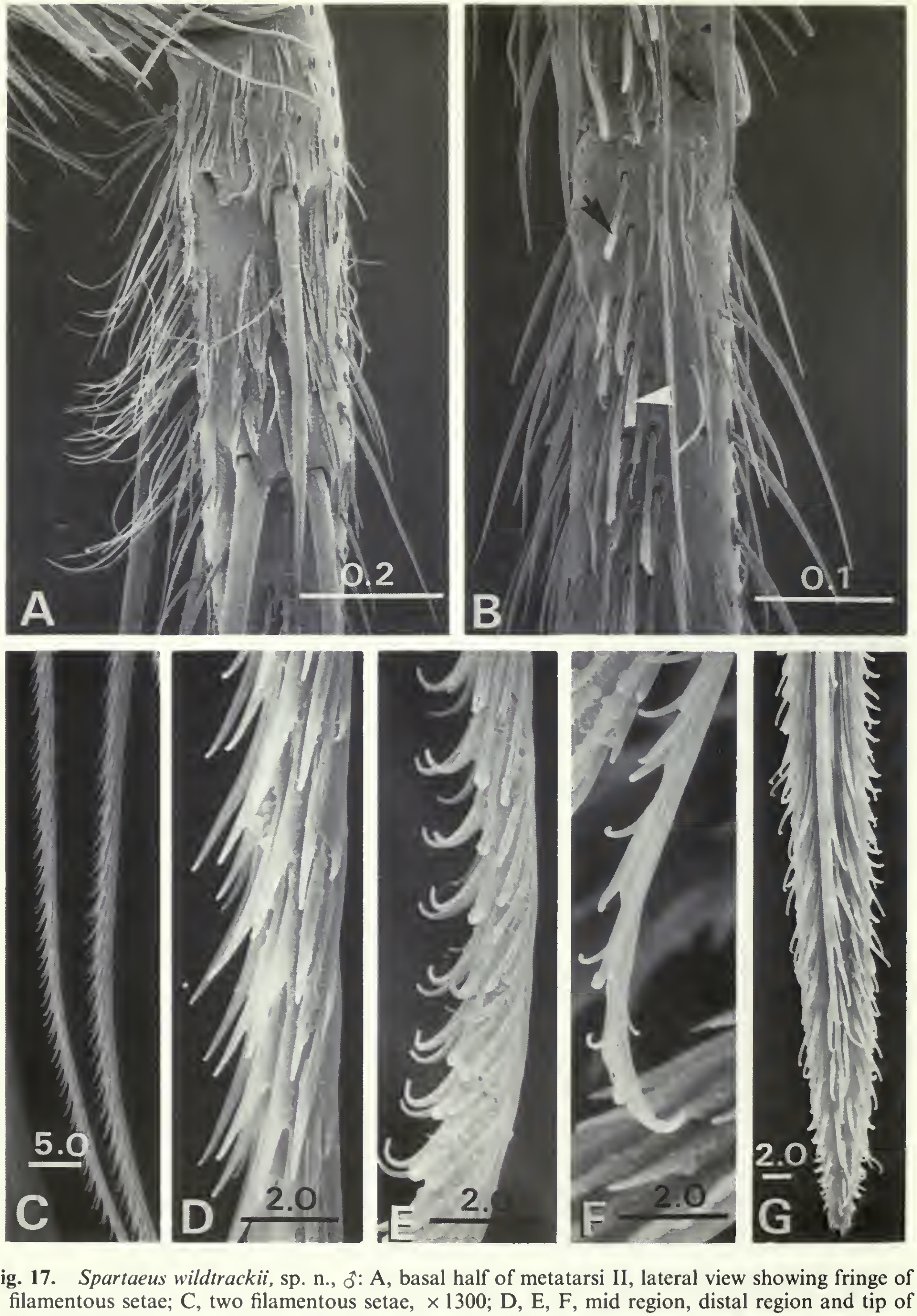

Fig. 17. *Spartaeus wildtrackii*, sp. n., ♂: A, basal half of metatarsi II, lateral view showing fringe of filamentous setae; C, two filamentous setae, × 1300; D, E, F, mid region, distal region and tip of filamentous setae, × 7000, × 8000, × 8000; B, basal half of tarsi II, ventral view showing row of prey capture setae, arrowed; × 210; G, detail of prey capture setae, × 2000. Scale bars μm.

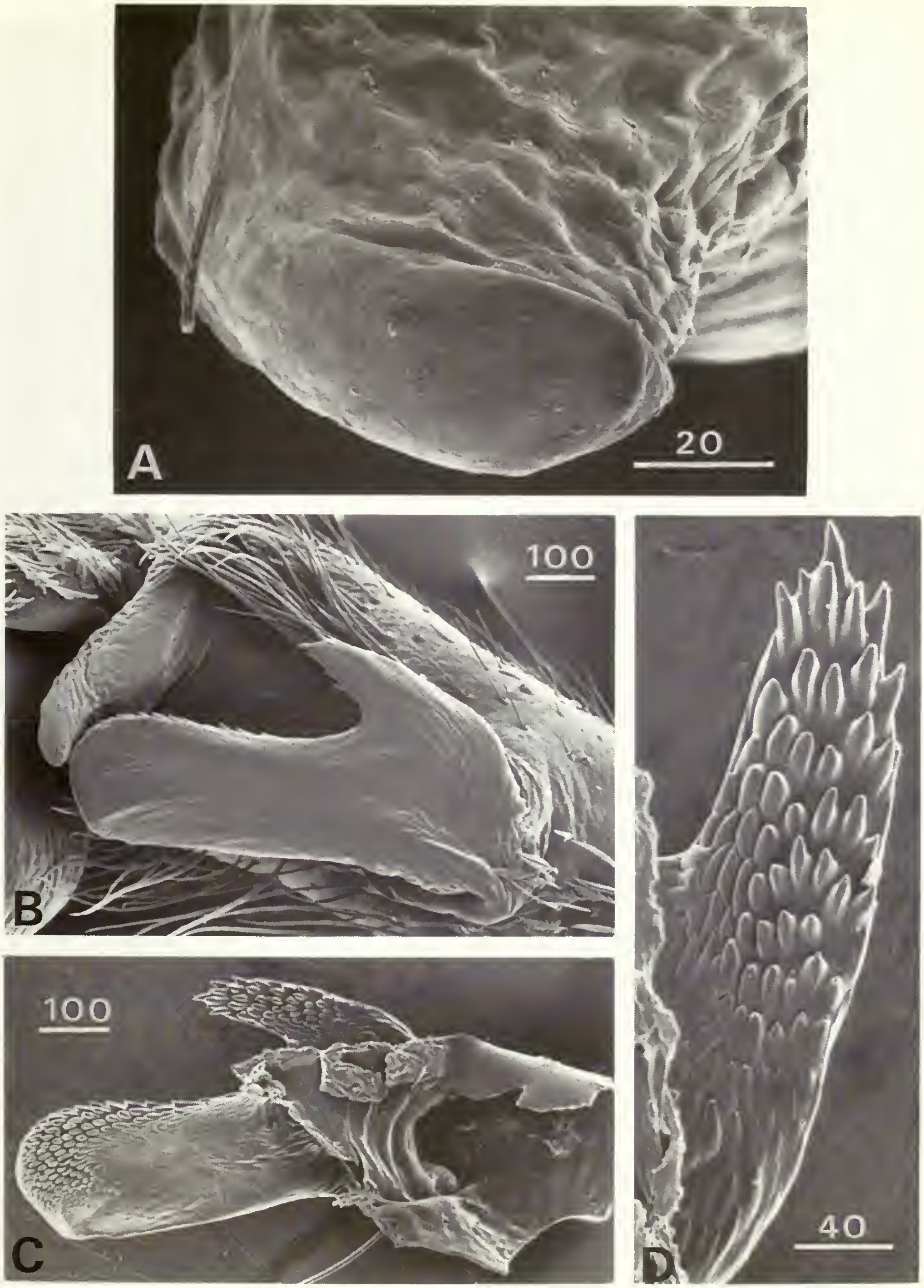

Fig. 18. *Spartaeus wildtrackii* sp. n., tibia of male palpal organ: A, ventral apophysis inner view, × 1000; B, retrolateral apophysis, outer view, × 100; C, retrolateral apophysis, inner view, × 100; D, detail of dorsal prong of retrolateral apophysis, × 350. Scale bars µm.

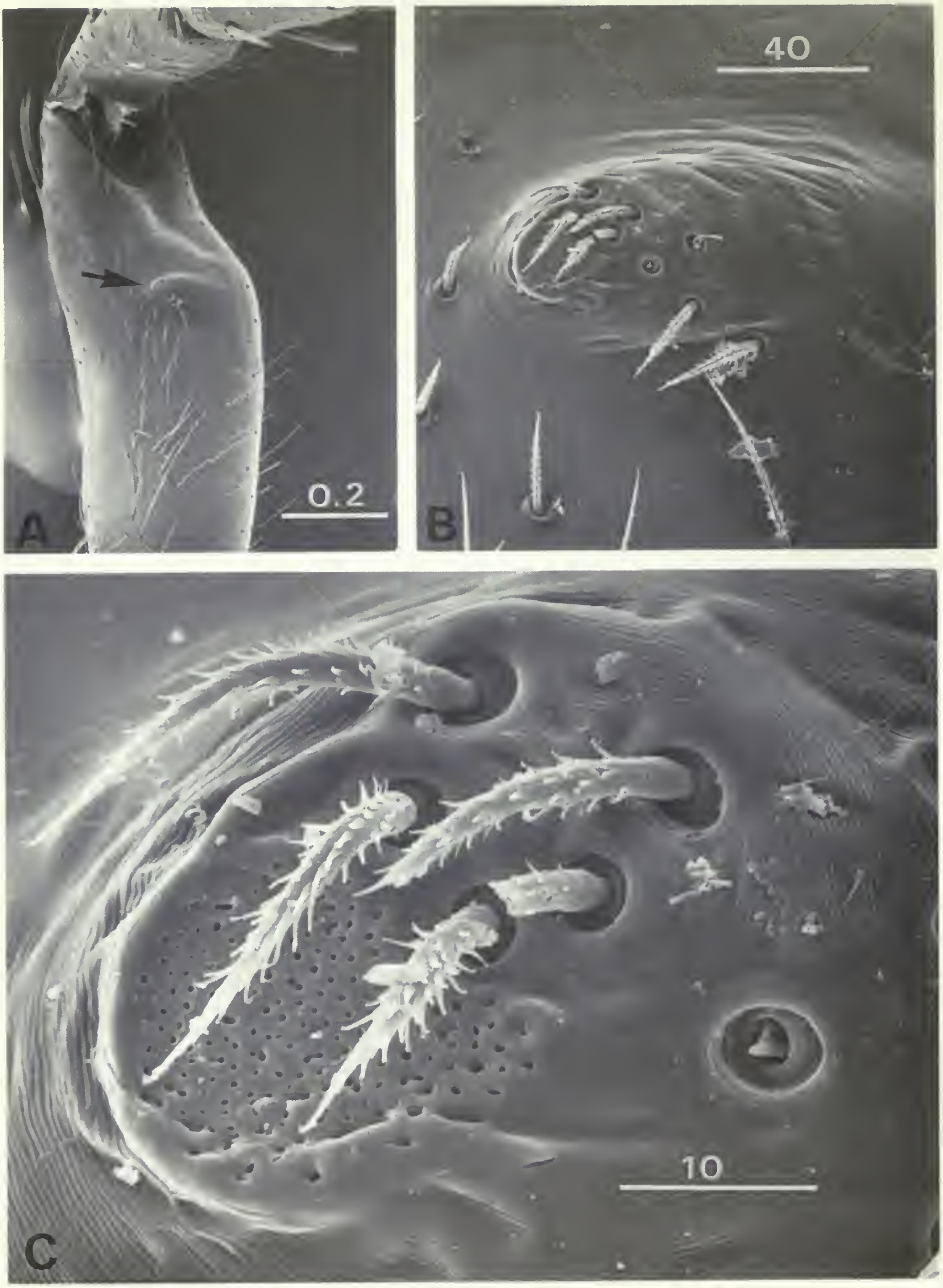

Fig. 19. *Mintonia caliginosa* sp. n., ♂: A, underside of femora I showing position of femoral organ, arrowed, × 75; B, femoral organ, × 550; C, femoral organ showing pores, × 2800. Scale bars A, mm; B, C, μm.

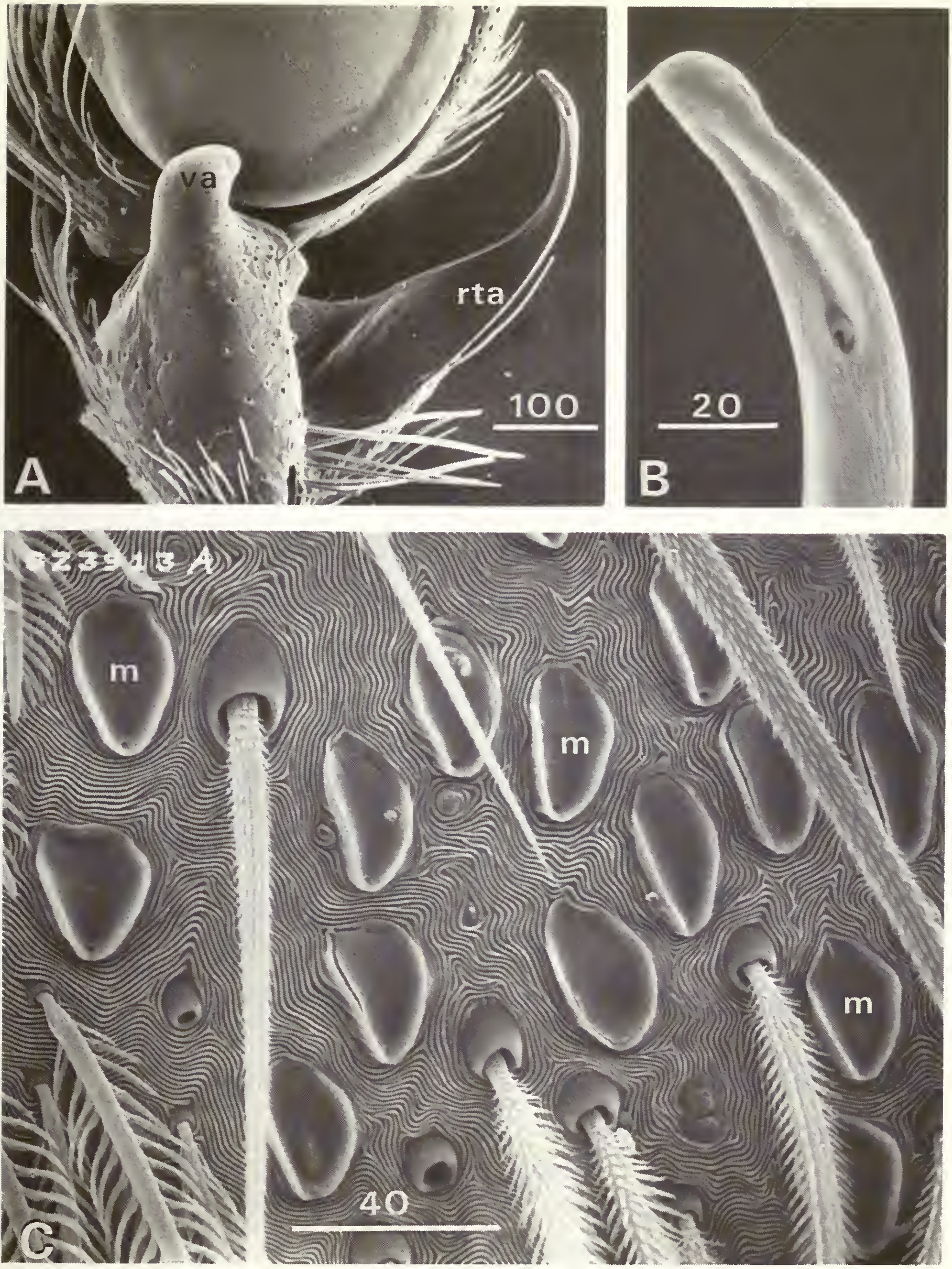

Fig. 20. (A, B) *Mintonia tauricornis* Wanless, ♂, palpal organ: A, tibia showing ventral apophysis and pore bearing retrolateral apophysis, × 150; B, tip of retrolateral apophysis showing pore, × 850. C, *Portia labiata* Thorell, ♂, showing mytiliform field on dorsal surface of abdomen, × 730. Abbreviations: m, mytiliform organs; va, ventral apophysis; rta, retrolateral tibial apophysis. Scale bars μm.

British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as on conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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Titles to be published in Volume 52

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Mites of the genus *Holoparasitus* Oudemans 1936 (Mesostigmata: Parasitidae) in the British Isles

Keith H. Hyatt

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Synopsis

The mites of the genus *Holoparasitus* Oudemans, 1936 occurring in the British Isles and the Channel Islands are revised. Five species are recorded of which two, *H. lawrencei* and *H. maritimus*, are new to science, and *H. calcaratus* (C. L. Koch, 1839) is recorded for the first time. A neotype is designated for *H. calcaratus*. Habitat and distribution data are given and keys to species for males and females are provided.

Introduction

The family Parasitidae comprises two subfamilies, the Parasitinae Oudemans, 1901 and the Pergamasinae Juvara-Bals, 1972. Hyatt (1980) has revised the British species of Parasitinae. Following Evans and Till (1979) the British Pergamasinae comprises the genera *Pergamasus* Berlese, 1904, *Amblygamasus* Berlese, 1904, *Paragamasus* Hull, 1918, *Holoparasitus* Oudemans, 1936 and *Pergamasellus* Evans, 1957. Of these, the first three were included by Bhattacharyya (1963) in his revision of the British species of *Pergamasus sensu lato,* whilst the monotypic genus *Pergamasellus* (of which specimens have so far been found only in two localities in southern England) is figured by Evans and Till (1979). The remaining genus, *Holoparasitus*, is revised in the present paper.

The genus *Holoparasitus* has been mentioned in the British literature scarcely a dozen times and only four authors, Halbert (1915), Hull (1918), Turk and Turk (1952) and Turk (1953), discussed their determinations. Halbert (1915) recorded *calcaratus* Koch, *pollicipatus* Berlese and *inornatus* Berlese from the west coast of Ireland, but he attached reservations to his identifications. Hull (1918) recorded the same three taxa from north-east England. Turk and Turk (1952) recorded *berlesei* Oudemans and commented on the confused synonymy of this species, echoing the remarks of Oudemans (1936), whilst Turk (1953), in his 'Synonymic Catalogue of British Acari', listed all the above names plus four of Berlese's 'varieties' based on specimens in his own collection. The remaining authors have given species determinations without comment. Where these specimens are available for study they are referred to under the taxa they are considered to represent.

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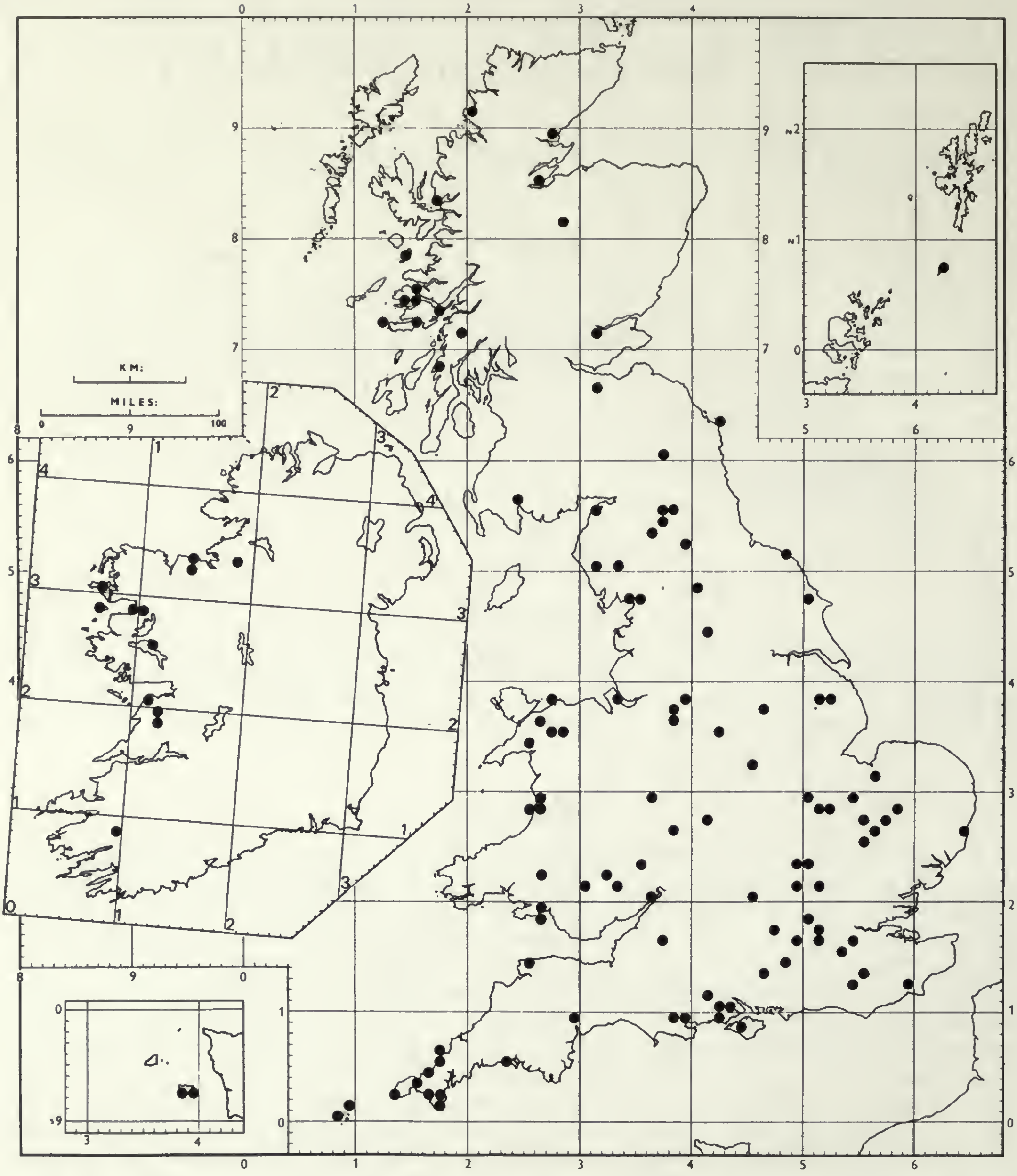

Fig. 1 The National and Irish Grids, showing to the nearest 10-kilometre square the extent of material examined during the preparation of the present work.

Mead-Briggs and Hughes (1966) recorded *Holoparasitus pollicipatus* from Cambridgeshire and Davis (1963) recorded *Holoparasitus* sp. from Northamptonshire. Unfortunately none of these specimens is available for study.

The most comprehensive revision of the European species of the genus is by Karg (1971) who keys and illustrates nine species of which three, *calcaratus, inornatus* and *stramenti* Karg, are represented in the British fauna.

Material

This revision is based on the examination of over six hundred specimens. The majority were removed from Berlese-funnel extractions during the course of my revision of the British Parasitinae (Hyatt, 1980). A few were removed from subsequent samples, mainly from areas of northern England and south-west Scotland not previously sampled. With the exception, however, of the monotypic genus *Pergamasellus, Holoparasitus* is not found so abundantly as the other genera of Pergamasinae, nor is it apparently so widely distributed.

Few named specimens were already in the Museum collections and of these the majority were in the J. H. Murgatroyd and Harry Britten collections from the New Forest area and the north of England respectively.

The map, figure 1, shows on the 10-kilometre squares of the National and Irish Grids the extent of the material from which I have examined *Holoparasitus* in the British Isles and the Channel Islands. Localities for Great Britain are given under the current English and Welsh counties and Scottish regions or island areas, but if a record is from only a small part of the area the former county name is inserted in parentheses. Additionally, large urban areas, e.g. Manchester and London, and islands or individual but prominent localities, e.g. Isle of Wight, Island of Mull, or Dungeness, are given as such.

External morphology

The external morphology of *Holoparasitus* is essentially typical of the Parasitidae and the terms used in the descriptions follow Evans and Till (1979) and Hyatt (1980). As in the majority of the Pergamasinae the dorsal setae of the idiosoma are usually of uniform length and thickness, whereas in the majority of species of Parasitinae these setae are heterogeneous. *Holoparasitus* species are usually readily separated from the other pergamasines by being conspicuously more spherical in body outline, and even under low magnifications the ventral fusion of the holodorsal and opisthogastric shields in the British species of *Holoparasitus sensu stricto* is easily seen. The exception to this last character is in the subgenera *Ologamasiphis* Holzmann, 1969 and *Heteroparasitus* Juvara-Bals, 1976 (both as yet not recorded from the British Isles) in which the two shields are not fused, although the holodorsal shield is continued ventrally, unlike *Pergamasus sensu lato* which has the holodorsal shield entirely dorsal.

Summary of classification

Oudemans (1936) proposed *Holoparasitus* as a new name for *Ologamasus* Berlese, 1906 (= *Hologamasus* [lapsus] Berlese, 1892) with the type species *Gamasus calcaratus* C. L. Koch, 1839. The type species of *Ologamasus* Berlese, 1888 is, by monotypy, *Gamasus aberrans* Berlese, 1888, a member of the family Rhodacaridae (Ryke, 1962, Lee, 1970).

The first comprehensive review of the genus *Holoparasitus* was contained in Berlese's 'Monografia del genere *Gamasus* Latr.' published in 1906. In this work the following ten taxa are recognised: *Gamasus (Ologamasus) calcaratus* Koch, 1839 and its two varieties, *excisus* Berlese, 1906 and *siculus* Berlese, 1906; *Gamasus (Ologamasus) inornatus* Berlese, 1906; *Gamasus (Hologamasus) pollicipatus* Berlese, 1904 and its five varieties *appeninorum, cultriger, excipuliger, peraltus,* and *pseudoperforatus,* all Berlese, 1906.

Oudemans (1936) considered that Berlese's *pollicipatus* and Koch's *calcaratus* were both synonyms of the earlier *Acarus lichenis* Schrank, 1781. However, Micherdzinski (1969) considered that Oudemans had no real evidence for this, bearing in mind that Schrank's figures were so lacking in detail.

Of the recent authors Holzmann (1969) uses the name *Ologamasus* Berlese, 1892, with which she erroneously considers *Holoparasitus* to be synonymous. She recognises two subgenera, *Ologamasus s. str.* and *Ologamasiphis* nov., separated by several characters of the deutonymph and the female. In the subgenus *Ologamasus s. str.* she includes *calcaratus* Koch, 1839, *inornatus* Berlese, 1906, *hemisphaericus* Vitzthum, 1923, *absoloni* Willmann, 1940 and *intermedius* Holzmann, 1969, whilst in *Ologamasiphis* she includes *rotulifer* Willmann, 1940 and a new species, *minimus* Holzmann, 1969.

Micherdzinski (1969) follows Oudemans in his preference for *Holoparasitus* and divides the genus into four species-groups: 1. *calcaratus*-group and 2. *pollicipatus*-group, both based on the form of the femoral spurs on leg II of the male, 3. *Ologamasiphis*-group with *H. rotulifer* and *H. minimus* following Holzmann, and 4. a group to include females which do not belong to previous groups, *H. excisus* (Berlese) and *H. hemisphaericus* (Vitzthum).

Karg (1971), at couplet twelve in his key to females, recognises the subgenus *Ologamasiphis* for three species, *minimus* Holzmann, *coronarius* Karg (nom. nov. pro *rotulifer* Holzmann, 1969, non Willmann, 1941) and *tirolensis* Sellnick, 1968, implying that the preceding species belong to *Holoparasitus s. str.*

Genus *HOLOPARASITUS* Oudemans

Hologamasus Berlese, 1904: 235. Non Berlese, 1892: 62.
Ologamasus Berlese, 1906: 242. Non Berlese, 1888: 194.
Holoparasitus Oudemans, 1936: 164.

TYPE SPECIES: *Gamasus calcaratus* C. L. Koch, 1839.

Dorsal and ventral shields of the adults well sclerotised; males with holodorsal and opisthogastric shields always fused posteriorly; females with holodorsal and opisthogastric shields fused posteriorly in *Holoparasitus s. str.*, but free in the subgenus *Ologamasiphis* Holzmann. Deutonymphs with separate podonotal and opisthonotal shields, not strongly sclerotised. In all stages setae of dorsal hexagon, i.e. *j5, z5* and *j6*, similar to each other and not differing markedly from the remaining dorsal stage which are generally short (not exceeding 50 µm) and often inconspicuous. Tritosternum of male biramous and sometimes modified, base closely associated with genital orifice. Tristosternum of deutonymph and female normal, biramous. Junction between sternal and metasternal shields of female olique. Genital shield of female broadly pentagonal. Opisthogaster with usually not more than 15 pairs of setae. Setae *al* of palp trochanter bifid and with one or more distinct slender processes; setae al_1 and al_2 of palp femur entire, spatulate or setiform. Corniculi strong, entire or notched internally. Legs of deutonymph and female without spurs; only leg II of male spurred. Lobes of pulvilli normal, rounded.

Key to species

Males

1 Apophysis on femur II thumb-shaped, about twice as long as axillary process (Fig. 2G) . . . 2
– Apophysis on femur II short, hemispherical and not extending beyond the blunt axillary process (Fig. 8G) . . . 3
2 Sternogenital shield with a conspicuous 'excipulum' medially between coxae II and III (Fig. 2B); majority of dorsal setae extremely short (*c.* 10–20 µm) (Fig. 2A); idiosoma 590–635 µm . . . ***Holoparasitus calcaratus*** (C. L. Koch) (p. 143)
– Sternogenital region without such a median 'excipular' mark; dorsal setae generally exceeding 25 µm in length; idiosoma 520–570 µm . . . ***Holoparasitus stramenti*** Karg (p. 146)
3 Anterior margin of sternogenital shield strongly concave medially to behind sternal setae I; a conspicuous and shallow transverse structure line present at sternal setae II (Fig. 8B); idiosoma 530–590 µm . . . ***Holoparasitus inornatus*** (Berlese) (p. 151)
– Anterior margin of sternogenital shield not strongly concave medially; sternal ornamentation otherwise; idiosoma exceeding 680 µm . . . 4
4 Large species – idiosoma 780–840 µm; sternal region with a light but strongly procurved line reaching forward from sternal setae II (Fig. 10B); tectum trispinate, centre spine long (Fig. 10C); corniculi smooth . . . ***Holoparasitus lawrencei*** sp. n. (p. 155)
– Smaller species – idiosoma 680–750 µm; sternal region with reticulations only; tectum broadly triangular, granular (Fig. 13C); corniculi cleft on inner margins (Fig. 13G) . . . ***Holoparasitus maritimus*** sp. n. (p. 158)

Females

1 Genital shield produced anteriorly to a tongue-shaped apex (Fig. 6B); endogynium as in figure 6C; idiosoma 590–670 µm . . . . ***Holoparasitus stramenti*** Karg (p. 146)

– Genital shield with anterior margin forming an obtuse to right angle, with or without a small protruding tip (Fig. 9B) 2

2 Sternal shield divided longitudinally into two (Fig. 9B); endogynium appears as a circular granular structure (Fig. 9C); idiosoma 610–690 µm . . . ***Holoparasitus inornatus*** (Berlese) (p. 151)

– Sternal shield entire (Fig. 11B) 3

3 Sternal shield with a pair of indentations on the anterior margin internally to sternal setae I (Fig. 3B); endogynium as in figure 3C; majority of dorsal setae extremely short (*c.* 10–25 µm) (Fig. 3A); idiosoma 670–720 µm . . . . . . ***Holoparasitus calcaratus*** (C. L. Koch) (p. 143)

– Sternal shield with anterior margin smooth, without indentations 4

4 Sternal shield granular, with a distinct median pattern, pre-sternal shields entire or divided, strongly denticulate (Fig. 14B); endogynium as in figure 14C; idiosoma 770–810 µm . . . . ***Holoparasitus maritimus*** sp. n. (p. 158)

– Sternal shield smooth, no distinct median pattern; pre-sternal shields entire or divided, granular (Fig. 11B); endogynium as in figure 11C; idiosoma 850–920 µm . . . . ***Holoparasitus lawrencei*** sp. n. (p. 155)

Descriptions of species

Holoparasitus calcaratus (C. L. Koch)
(Figs 2A–G, 3A–G)

Gamasus calcaratus C. L. Koch, 1839: Heft 26, Taf. 6.
Gamasus timidulus C. L. Koch, 1839: Heft 26, Taf. 7.
Gamasus (Ologamasus) calcaratus: Berlese, 1906: 245.
Holoparasitus calcaratus: Micherdzinski, 1969: 354.
Ologamasus (Ologamasus) calcaratus: Holzmann, 1969: 47.
Holoparasitus excipuliger: Karg, 1971: 361. Non Berlese, 1906.
Ologamasus pollicipatus Berlese, 1904; 1913: 203 (in part).

Designation of a neotype

Oudemans (1906, 1929, 1936) opined that *Gamasus timidulus* C. L. Koch (♀) and *Gamasus calcaratus* C. L. Koch (♂) were junior synonyms of *Acarus lichenis* Schrank, 1781. However, Schrank's and Koch's specimens are no longer in existence and although Michердzinski (1969) and Karg (1971) have accepted that *timidulus* is a synonym of *calcaratus*, they have not accepted the validity of *lichenis*. Since Oudemans (1936) it has been universally accepted that *calcaratus* is the type of *Holoparasitus*, but, unfortunately, authors' concepts of *calcaratus* have not been consistent. Specimens labelled *Ologamasus pollicipatus* in the set of slides accompanying the *Acarotheca Italica* (Berlese, 1913) in the BM(NH) collection are referable to the present species, whereas the specimens similarly labelled in the set in the Oudemans collection are *rotulifer* Willmann, 1940.

Through the courtesy of Dr L. van der Hammen I have been able to examine material from several places very close to Regensburg, the type locality. Of the 15 samples of Gamasina examined, seven contained *Holoparasitus* and of these six contained specimens of *H. calcaratus*. One sample contained a single male and female of another species.

A female from Dechbetten, 1·5 miles (2 km) west of Regensburg, Bavaria, 19 July 1959, in rotting dry litter, L. van der Hammen coll., is designated as the neotype of *Gamasus calcaratus* C. L. Koch. The specimen is deposited in the Rijksmuseum van Natuurlijke Historie, Leiden, together with deutonymphs, males and other females from the same sample. Three males, three females and one deutonymph from this sample are retained in the British Museum (Natural History) through the courtesy of Dr van der Hammen.

MALE. The holodorsal and opisthogastric shields, which are fused ventrally posterior to coxae IV, are strongly sclerotised and completely reticulated (Figs 2A, B). The dorsum (Fig. 2A) measures 590–635 µm long × 430–480 µm wide and bears over 50 pairs of simple setae ranging in length from

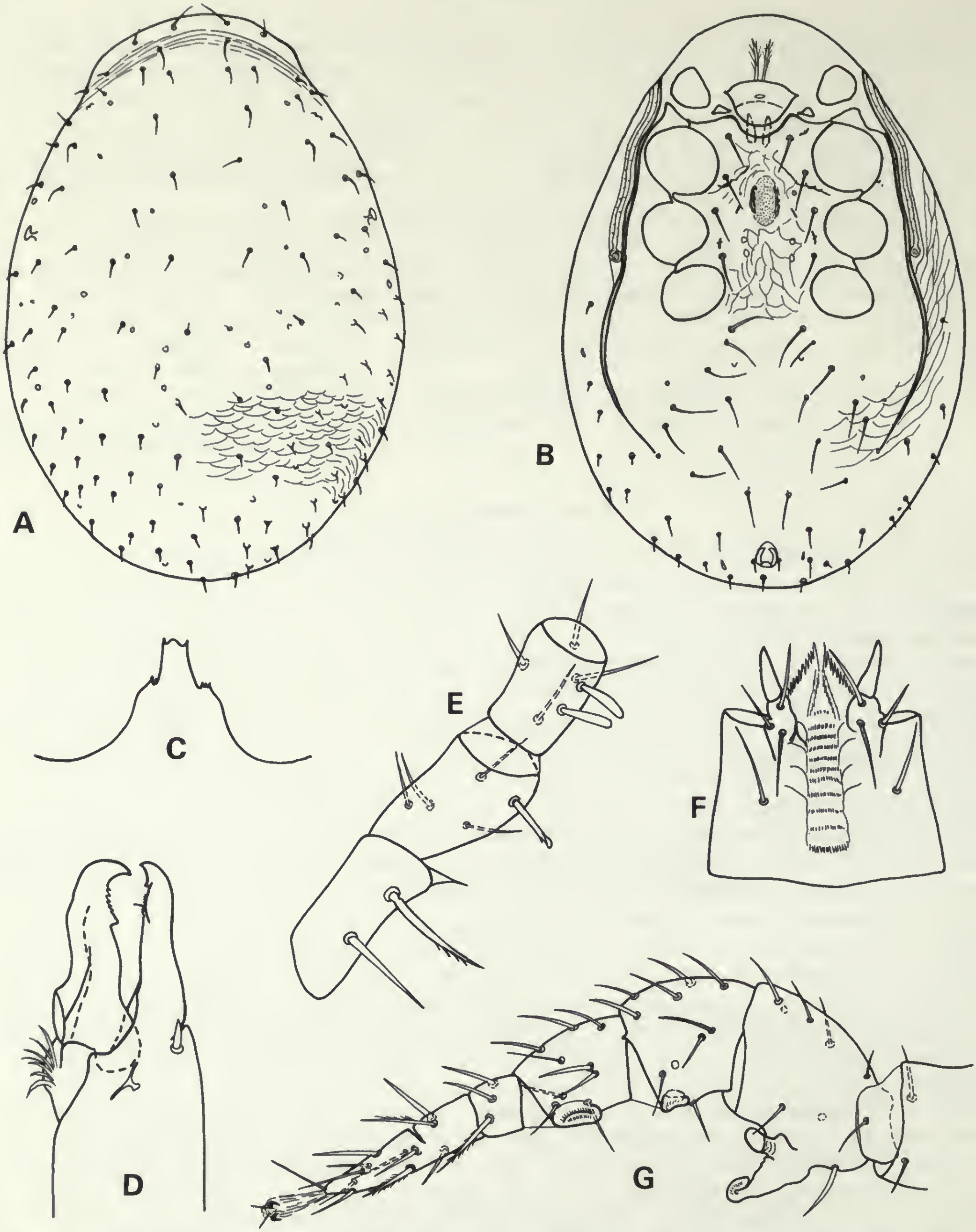

Fig. 2 *Holoparasitus calcaratus* (C. L. Koch), **male** – A dorsum, B venter, C tectum, D chelicera, E palp trochanter, femur and genu, F venter of gnathosoma, G leg II.

35 µm (the vertical setae, *j*1) to 10 µm or less for the majority in the opisthonotal region. The setae are not arranged entirely symmetrically.

The tritosternum comprises two slender pilose laciniae that arise from below the anterior margin of the genital lamina (Fig. 2B). The sternogenital region is strongly reticulated and bears medially between coxae II and III a conspicuous oval mark (the 'excipulum' of Berlese). The sternogenital

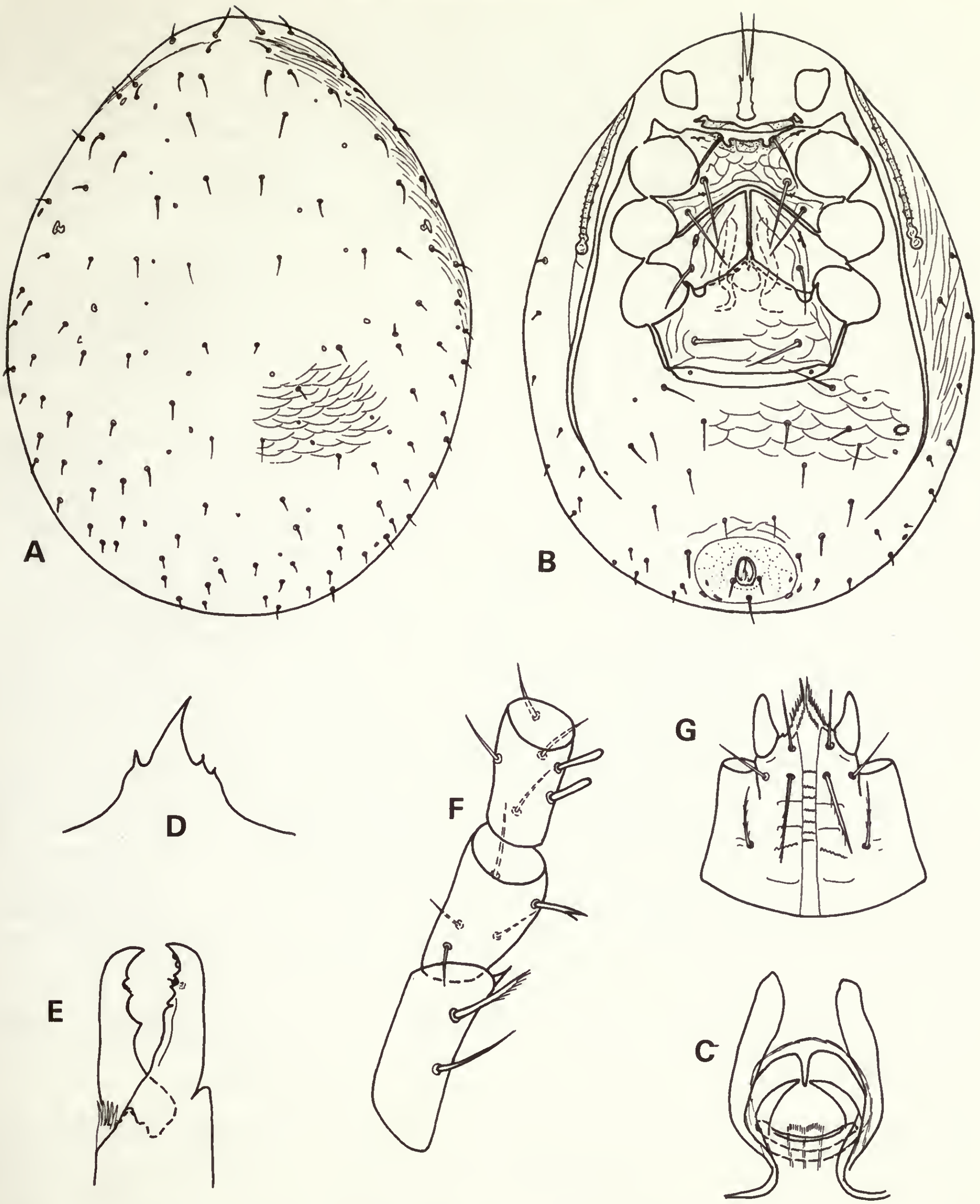

Fig. 3 *Holoparasitus calcaratus* (C. L. Koch), **female** – A dorsum, B venter, C endogynium, D tectum, E chelicera, F palp trochanter, femur and genu, G venter of gnathosoma.

and median opisthogastric setae are up to 40 μm in length, whilst the three anal setae and those situated posteriorly in the opisthogastric region are as little as 10 μm. The stigma is situated opposite the posterior margin of coxa III and the peritreme extends anteriorly to coxa I.

The tectum is shown in figure 2C. The median portion is broad and blunt in all specimens examined and the lateral teeth vary. The chelicera is shown in detail in figure 2D. The movable digit is 75 µm long and bears one large tooth and 5–6 small, sometimes irregular, teeth. The fixed digit bears one sometimes blunt tooth towards the tip and up to seven very small teeth in the region of the pilus dentilis. The palp trochanter, femur and genu are shown in figure 2E. The anterolateral setae of the femur and genu are spatulate, that on the genu is more slender and is bifurcate near to its tip. The corniculi (Fig. 2F) are strong and stalked and all the gnathosomal setae are simple. Leg II is shown in detail in figure 2G. The femoral apophysis is thumb-shaped and is about twice as long as the axillary process. The ventral process on the genu is short and rounded whilst that on the tibia is elongate and bean-shaped. All leg setae are slender whilst a number on the tarsi of legs II–IV are stronger and pilose on one margin. The ambulacra are normal.

FEMALE. The holodorsal and opisthonotal shields, which are strongly sclerotised and completely reticulated, are fused ventrally anterior to the anus (Figs 3A, B). The dorsum (Fig. 3A) measures 670–720 µm long × 500–560 µm wide and bears up to 57 or more pairs of simple setae, about 20 pairs being in the podonotal region and from 34–37 pairs in the opisthonotal region. The vertical setae, *j1*, are the longest and measure *c.* 40 µm, whilst the shortest setae, the majority of those in the opisthonotal region, measure as little as 10 µm and are extremely fine.

The tritosternum (Fig. 3B) has a narrow base and the paired laciniae are simple. The presternal shields are fused to form a single narrow bar. The ventral shields are strongly reticulated and all setae are simple. The sternal shield has a pair of indentations on the anterior margin inwards from sternal setae I. The reticulations show a bold procurved transverse line extending from posterior to coxae II through sternal pores II. The genital shield measures 130–160 µm long × 210–220 µm wide. Its anterior margin is formed into a slight obtuse angle or right angle and bears a slender pointed tip. The endogynium is shown in figure 3C and in the specimens examined shows constancy in form despite clearing for examination. The opisthogastric region bears 8–9 pairs of setae. The longest of the ventral setae are sternal setae II and III which measure up to 75 µm. The shortest ventral setae are around the posterior margin and measure 10 µm or less. In most of the specimens examined the outline of the deutonymphal anal shield is retained. The stigma is situated opposite the posterior margin of coxa III and the peritreme extends anteriorly to coxa I.

The tectum (Fig. 3D) has the centre portion tapered and sinuous. The chelicera is shown in figure 3E. The movable digit measures 87 µm and bears three prominent teeth and two small teeth, whilst the fixed digit bears five teeth decreasing in size towards its tip. The palp trochanter, femur and genu are shown in figure 3F. The anterolateral seta of the genu is bifurcate whilst those of the tibia are spatulate. The venter of the gnathosoma is shown in figure 3G. The internal posterior hypostomatic setae are the longest (70 µm or more) and with the palpcoxal setae are pilose, at least on one margin. The hypognathal groove shows only about seven rows of denticles. The leg setae are slender and a few on the tarsi are pilose on one margin. The ambulacra are normal.

MATERIAL EXAMINED. 14 samples – 7 ♂♂, 16 ♀♀.

ENGLAND: Hampshire, Surrey, Sussex/Kent border near the coast, Cambridgeshire (including Huntingdonshire).

This species is recorded mainly from grasses and leaf-litter in damp habitats.

As far as I can establish, there are no previous authenticated records from the British Isles.

Holoparasitus stramenti Karg
(Figs 4A–F, 5A–G, 6A–G)

Holoparasitus stramenti Karg, 1971: 356.
Gamasus (Ologamasus) calcaratus var. *excisus* Berlese, sensu Halbert, 1915: 54 (in part).
Gamasus (Ologamasus) pollicipatus Berlese, sensu Halbert, 1915: 55.
Holoparasitus pollicipatus (Berlese) sensu Browning, 1956: 386.

DEUTONYMPH. The lightly reticulated dorsal shields are weakly sclerotised and yellowish-brown in colour. The podonotal shield averages 235 µm long × 325 µm wide. It bears 17 pairs of simple slender setae, none longer than 30 µm (Fig. 4A). The opisthonotal shield averages 180 µm long × 225 µm wide and bears 12 pairs of simple slender setae from 20–25 µm in length. The surrounding membrane bears dorsally on each side about 20 short, simple setae.

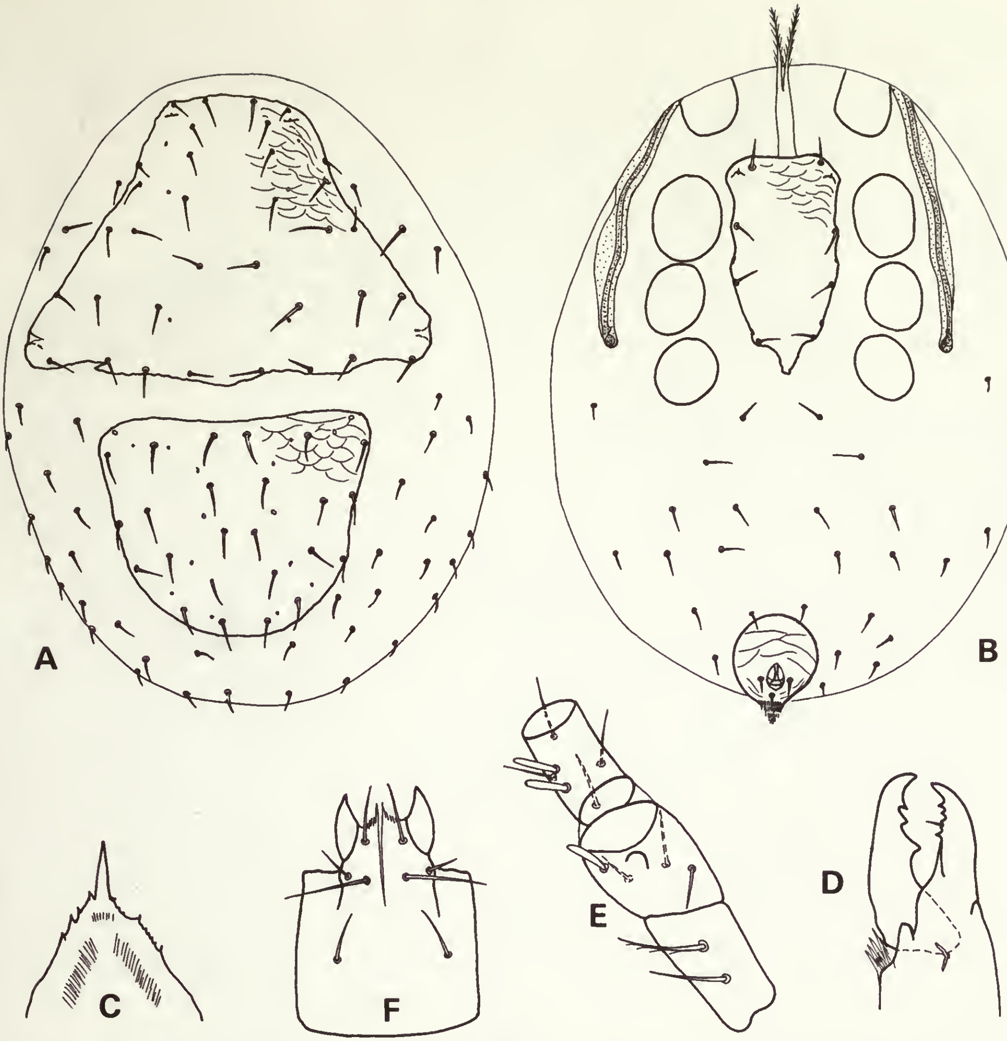

Fig. 4 *Holoparasitus stramenti* Karg, **deutonymph** – A dorsum, B venter, C tectum, D chelicera, E palp trochanter, femur and genu, F venter of gnathosoma.

The tritosternum has a narrow base and pilose laciniae. The sternal shield (Fig. 4B) averages 180 μm long and is lightly reticulated and weakly sclerotised. The sternal setae average 25 μm long and are simple. Pre-sternal shields absent. The oval anal shield bears the usual three setae, each simple and about 12 μm in length. The stigma is situated opposite the anterior margin of coxa IV, and the granular peritreme and peritrematal shield extend anteriorly to the level of coxa I. The 11 to 15 or more pairs of simple opisthogastric setae are slender.

The triangular tectum is serrated anteriorly and bears a slender tip (Fig. 4C). The chelicerae are as in figure 4D, the movable digit measures 58 μm in the figured specimen. The palp trochanter, femur and genu are shown in figure 4E. The anterolateral setae of the femur and genu are spatulate. The corniculi and the venter of the gnathosoma are as in figure 4F, the gnathosomal setae being simple with the internal hypostomatics the longest. The hypognathal denticles are not discernible. All leg setae are slender, the majority are simple but some, especially on tarsus II, are finely pilose on one margin. The pulvilli are normal, rounded and with two claws.

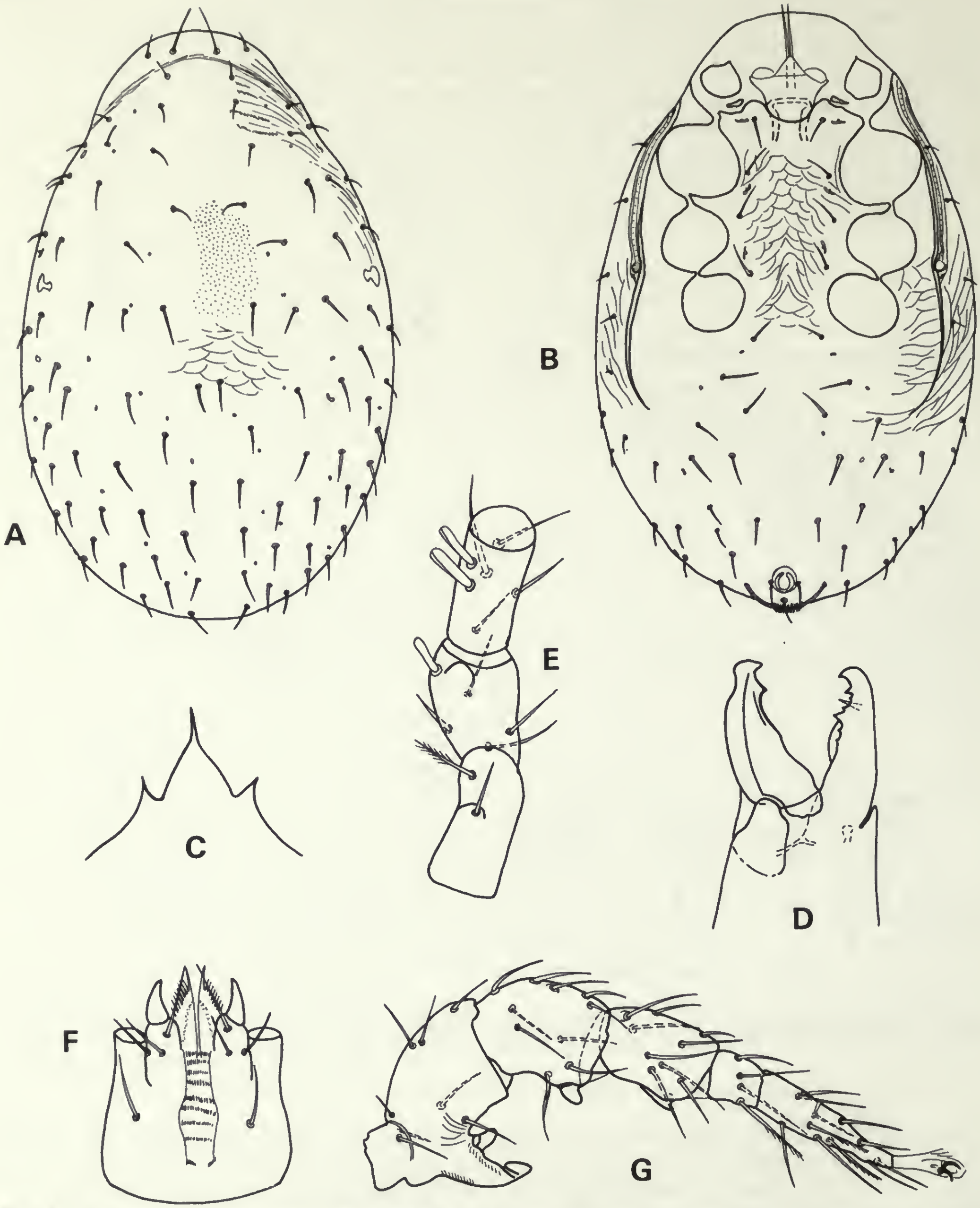

Fig. 5 *Holoparasitus stramenti* Karg, **male** – A dorsum, B venter, C tectum, D chelicera, E palp trochanter, femur and genu, F venter of gnathosoma, G leg II.

MALE. The holodorsal and opisthogastric shields, which are strongly sclerotised and completely reticulated, are fused ventrally anterior to the anus (Figs 5A, B). The dorsum (Fig. 5A) measures 520–570 μm long × 330–400 μm wide, is finely granular and bears 45 pairs of simple setae, 20 pairs in the podonotal region and 25 pairs in the opisthonotal region. The vertical setae, *j1*, are the longest, measuring up to 45 μm. The remaining setae are 20–25 μm long.

The tritosternum comprises two slender laciniae which arise from below the anterior margin of the genital lamina (Fig. 5B). The sternogenital region is reticulated and the pattern is constant for the species. The sternogenital setae and the median opisthogastric setae are the longest – up to 45 µm – whilst the remainder are considerably shorter. The three anal setae are simple. The stigma is situated opposite the posterior margin of coxa IV and the peritreme extends to coxa I.

The tectum (Fig. 5C) is normally symmetrically formed and is trispinate. The chelicera is shown in figure 5D; the movable digit is 50 µm long in the figured specimen and bears a single tooth near the tip, whilst the fixed digit bears two prominent teeth and about four smaller ones. The palp trochanter, femur and genu are shown in figure 5E. The anterolateral setae of the femur and genu are spatulate. The venter of the gnathosoma is as in figure 5F. The corniculi are stalked and strong. The gnathosomal setae are simple and the hypognathal groove bears about nine rows of denticles. Leg II is shown in detail in figure 5G. The femoral apophysis is strong and thumb-like whilst the axillary process is short, but elongate. The ventral process on the genu is swollen, whilst that on the tibia is not prominent. All the leg setae are slender, some on the tarsi being pilose on one margin. The ambulacra are normal, with rounded pulvilli and two claws.

FEMALE. The holodorsal and opisthogastric shields, which are strongly sclerotised and completely reticulated, are fused ventrally anterior to the anus (Figs 6A, B). The dorsum (590–670 µm long × 410–475 µm wide) is finely granular and bears 48–49 pairs of simple setae (Fig. 6A), 20 pairs in the podonotal region and 28–29 pairs in the opisthonotal region. The vertical setae, *j1*, are the longest, measuring up to 40 µm. The remaining setae are about 20–25 µm in length.

The tritosternum (Fig. 6B) has a narrow base and pilose laciniae. The presternal shields are fused to form a strong transverse bar, occasionally with a small section at each end being almost or entirely detached. The ventral shields are completely reticulated and are granular. The reticulations on the sternal shield follow a definite, but simple, pattern with a pair of oblique lines originating from the angle between coxae II and III and passing through sternal pores II, but petering out before reaching the centre of the shield. The genital shield measures 130–183 µm long × 190–225 µm wide, its size appearing to be related to the actual size of the specimen. The genital shield is unique among the British species of the genus in that it is produced anteriorly into a strong tongue-shaped apex. The endogynium is shown in figure 6C; its general content appears constant, but the position of the 'teeth' varies considerably due to distortion in life or during preparation for examination. The opisthogastric region bears 8–9 pairs of setae. The sternal setae are the longest – *c.* 45 µm – and the metasternal, genital and opisthogastric setae decrease slightly in length in that order. The three anal setae are short (*c.* 12 µm) and simple. The stigma is situated opposite the posterior margin of coxa III and the peritreme extends anteriorly to the level of coxa I.

The tectum (Fig. 6D) is similar to that of the male, but in some specimens irregularity is present. The chelicera is as in figure 6E. The movable digit measures 82 µm in the figured specimen and bears three teeth, whilst the fixed digit bears up to six less prominent teeth. The palp trochanter, femur and genu are shown in figure 6F. The anterolateral setae of the femur and genu are spatulate. The venter of the gnathosoma is shown in figure 6G. The palpcoxal setae are pilose on one margin whilst the other gnathosomal setae are simple. The hypognathal groove bears about eight rows of denticles. Some of the leg setae are finely pilose on one margin. The ambulacra are normal.

MATERIAL EXAMINED. 93 samples – 3 DNN, 80 ♂♂, 178 ♀♀.

ENGLAND: Isles of Scilly, Devon, Somerset, Berkshire, Hampshire, Surrey, Sussex, Kent, Middlesex, Hertfordshire, Buckinghamshire, Gloucestershire, Bedfordshire, Norfolk, Suffolk, Cambridgeshire (including Huntingdonshire), Hereford and Worcester, Leicestershire, Cheshire, North Yorkshire, Cumbria (Cumberland, Westmorland), Northumberland.

SCOTLAND: Lothian/Borders, Strathclyde (Argyllshire), Tayside (Perthshire), Inner Hebrides (Mull, Iona, Eigg).

WALES: Gwynedd (Caernarvonshire), Dyfed (Cardiganshire), Clwyd, Gwent, Glamorgan.

IRELAND: Galway, Mayo, Clare, Leitrim.

CHANNEL ISLANDS: Jersey.

Although this species has been collected from leaf-litter, compost, moss and grassland, it has a marked preference for wet, marshy habitats. One female from Co. Mayo, Ireland, was taken on the seashore.

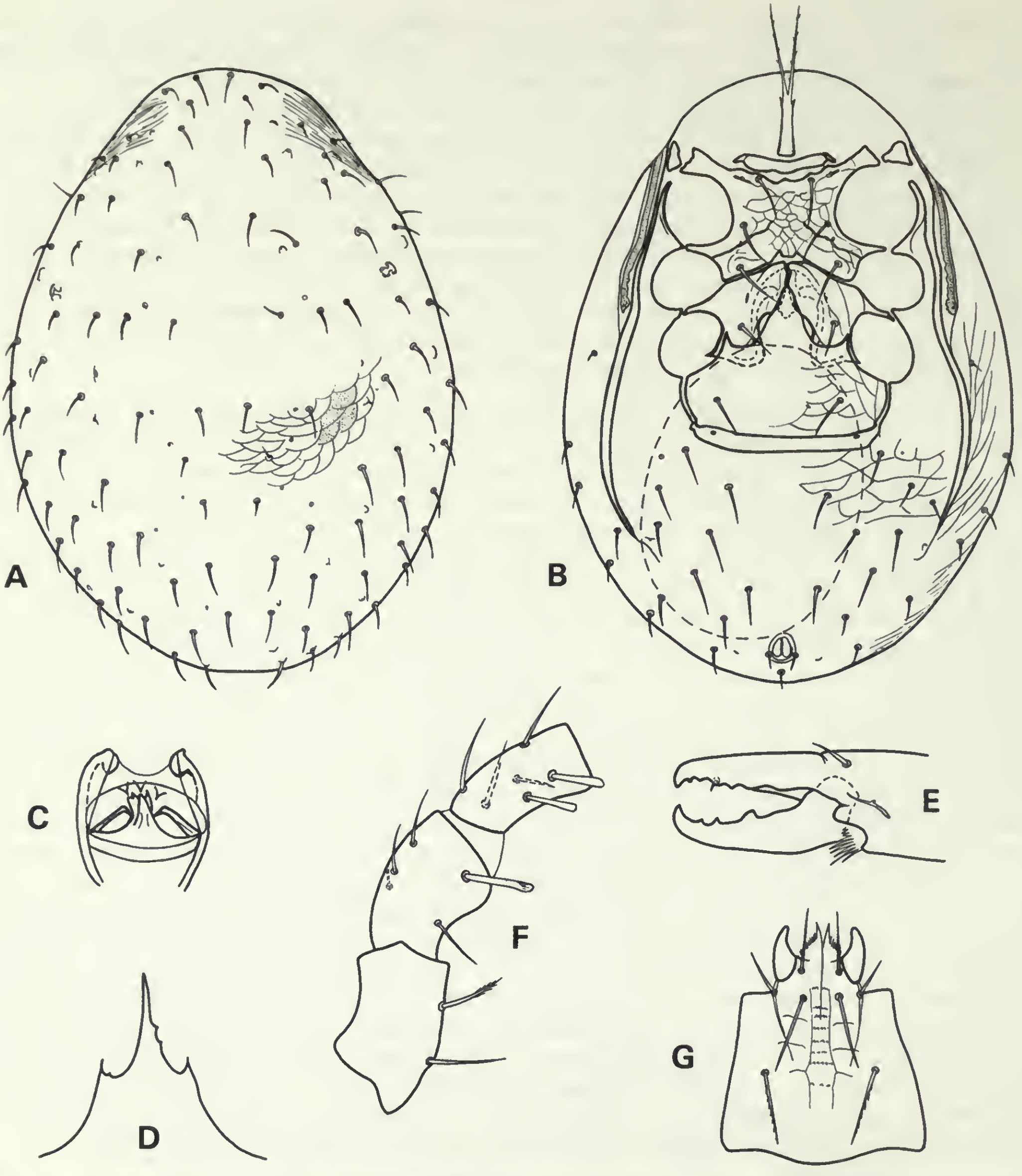

Fig. 6 *Holoparasitus stramenti* Karg, **female** – A dorsum, B venter, C endogynium, D tectum, E chelicera, F palp trochanter, femur and genu, G venter of gnathosoma.

Distribution. Karg (1971) stated that the holotype of this species came from the Baltic coast and gave its distribution as central Europe. The name has not appeared subsequently in the literature. *H. stramenti* is one of the two most abundant British members of the genus. It was recorded from Co. Mayo, Ireland, by Halbert (1915) as *Gamasus (Ologamasus) calcaratus* var. *excisus* Berlese from Achill Island and Westport, and as *Gamasus (Ologamasus) pollicipatus* Berlese from Clare Island. Two females of this species were recorded from Jersey by Browning (1956) as *Holoparasitus pollicipatus* (Berlese). A single undetermined female was recorded from Moor House National Nature Reserve, Westmorland, by Block (1965), whilst Davis (1970) recorded a single female from Monks Wood National Nature Reserve as *Holoparasitus ?pollicipatus*.

Holoparasitus inornatus (Berlese)
(Figs 7A–F, 8A–G, 9A–G)

Gamasus (Ologamasus) inornatus Berlese, 1906: 257.
Holoparasitus inornatus: Schweizer, 1961: 34 (♀ only), Micherdzinski, 1969: 366.
Ologamasus (Ologamasus) inornatus: Holzmann, 1969: 47.
Holoparasitus calcaratus (Koch, 1839) sensu Schweizer, 1961: 36 (♂ only). Karg, 1971: 361.
Gamasus (Ologamasus) calcaratus Koch, 1839 sensu Halbert, 1915: 54 (part).

DEUTONYMPH. The dorsal shields are light yellowish-brown in colour, weakly sclerotised and faintly reticulated (Fig. 7A). The podonotal shield averages 460 μm long × 300 μm wide when

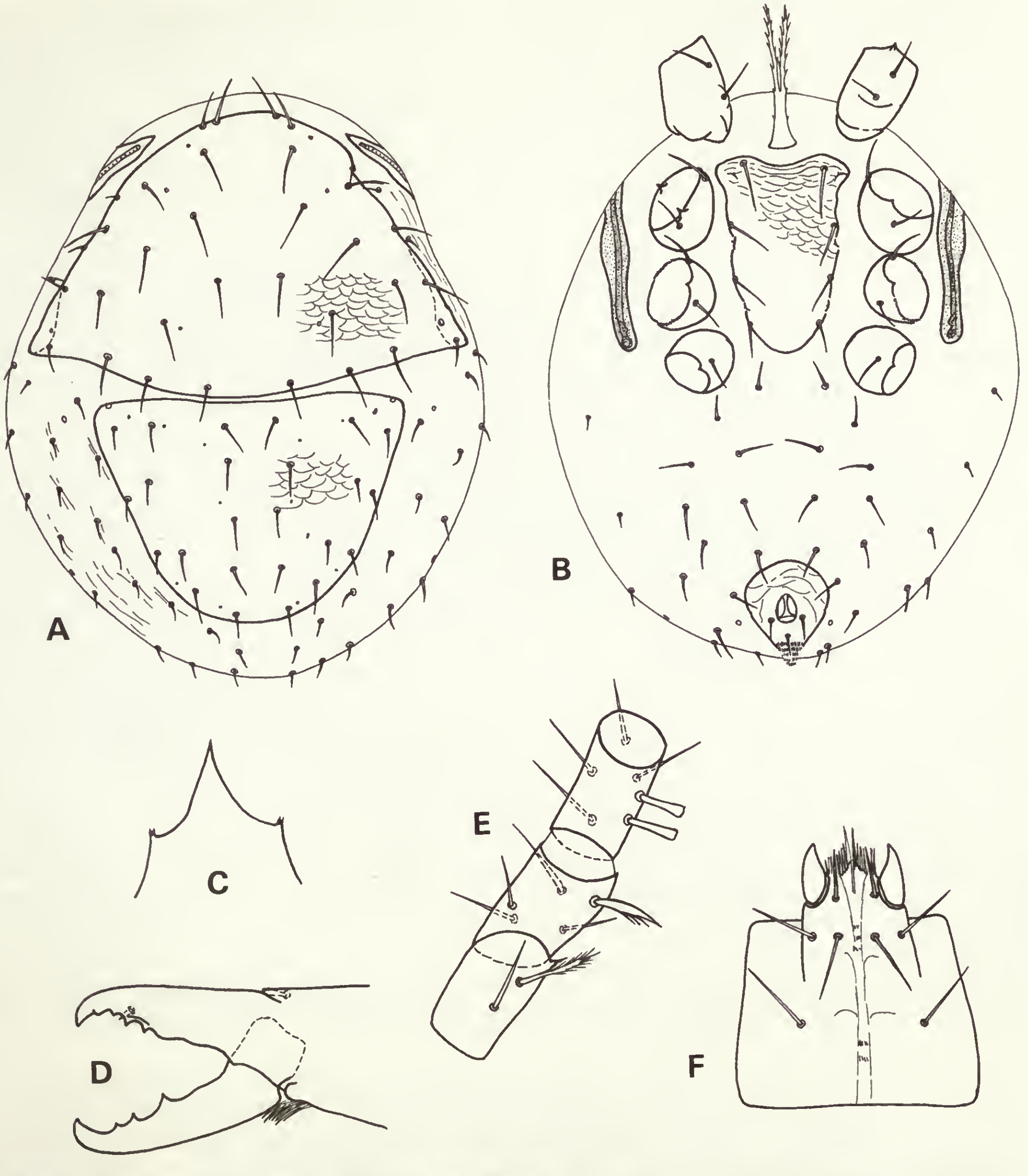

Fig. 7 *Holoparasitus inornatus* (Berlese), **deutonymph** – A dorsum, B venter, C tectum, D chelicera, E palp trochanter, femur and genu, F venter of gnathosoma.

flattened and depending on one or more of the marginal (*r*-series) setae being on or off the shield, bears 16–17 pairs of fine simple setae, none measuring more than about 35 µm. The opisthonotal shield averages 180 µm long × 210 µm wide and bears 12 pairs of simple setae up to *c.* 25 µm in length. All the dorsal setae taper extremely finely. The surrounding membrane bears dorsally on each side up to about 20 short simple setae.

The tritosternum has a narrow base and pilose laciniae. The sternal shield (Fig. 7B) measures 160–170 µm long and is lightly reticulated and weakly sclerotised. The setae are simple. Presternal shields absent. The oval anal shield bears the usual three setae, each simple and about 12–15 µm in length. The stigma is situated opposite the anterior margin of coxa IV and the granular peritreme and peritrematal shield extend anteriorly to the level of coxa I. The opisthogastric setae, which number about 17 pairs, are fine and simple.

The tectum (Fig. 7C) is triangular and is flanked by small tooth-like projections each side. The chelicera is shown in figure 7D; the movable digit measures 72 µm in the figured specimen and bears three teeth, whilst the fixed digit bears about five teeth. The palp trochanter, femur and genu are shown in figure 7E. The anterolateral seta of the femur is broad and pectinate on one margin and the two anterolateral setae of the genu are spatulate. The corniculi and venter of the gnathosoma are shown in figure 7F. The four pairs of gnathosomal setae are simple whilst the hypognathal denticles are indistinct. All leg setae are slender, the majority are simple, but a few on tarsus II are finely pilose on one margin. The ambulacra are normal, with rounded pulvilli and two claws.

MALE. The holodorsal and opisthogastric shields are fused ventrally posterior to coxae IV and are heavily sclerotised (Figs 8A, B). The dorsum, which measures 530–600 µm long × 390–460 µm wide, is strongly granular with almost no trace of reticulations (Fig. 8A). It bears, apparently, a fairly constant and symmetrically arranged number of setae, 20 pairs in the podonotal region and 30–31 pairs in the opisthonotal region. The longest setae, the verticals (*j1*), measure *c.* 30 µm and the tendency is for the setae to decrease in length towards the posterior of the dorsum where some are as short as 10 µm.

The tristosternum comprises a short base and two pilose laciniae (Fig. 8B). The sternogenital region is strongly reticulated and characteristically shaped. The anterior margin of the sternogenital shield is recessed deeply to accommodate the genital lamina and immediately posterior to sternal setae II there is a strong procurved ridge right across the shield. These two formations give this anterior region a very characteristic appearance. The posterior two-thirds of the sternogenital region are characteristically ornamented and are clearly separated from the opisthogastric region level with the posterior third of coxae IV, only the endopodal shields retaining their fusion. The sternogenital and opisthogastric setae are up to 50 µm in length, whilst the three anal setae and those around the posterior margin of the ventral surface are about 18 µm long. The stigma is situated opposite the posterior margin of coxa III and the peritreme extends anteriorly to coxa I.

The tectum is shown in figure 8C. The broad central part is acutely tapered and is flanked on each side by a short prong. The chelicera is shown in figure 8D. The movable digit is 83 µm long and bears four or five small teeth. The fixed digit bears six to eight small teeth. The palp trochanter, femur and genu are shown in figure 8E. The anterolateral setae of the genu and femur are spatulate. The corniculi (Fig. 8F) are strong and stalked and are cleft to a varying degree on their inner margins. The palpcoxal setae are finely plumose, the remaining three pairs of gnathosomal setae are simple. There are about 10 rows of hypognathal denticles. Leg II is shown in detail in figure 8G. The apophysis on femur II is short, hemispherical, and does not extend beyond the tip of the similarly shaped axillary process. The ventral processes on the genu and tibia are smooth and elongate. All leg setae are slender, some on tarsi II–IV are finely pilose on one margin. The ambulacra are normal.

FEMALE. The holodorsal and opisthonotal shields are fused ventrally posterior to coxae IV and are heavily sclerotised (Figs 9A, B). The dorsum (Fig. 9A), which measures 610–690 µm long × 420–570 µm wide, is strongly granular and, like the male, has almost no trace of reticulation. It bears about 50 pairs of simple setae, up to 23 pairs in the podonotal region and up to 27 pairs in the opisthonotal region. Setae *j1*, the verticals, are the longest, measuring about 35 µm and the remainder are slightly shorter with a minimum length of *c.* 18 µm posteriorly.

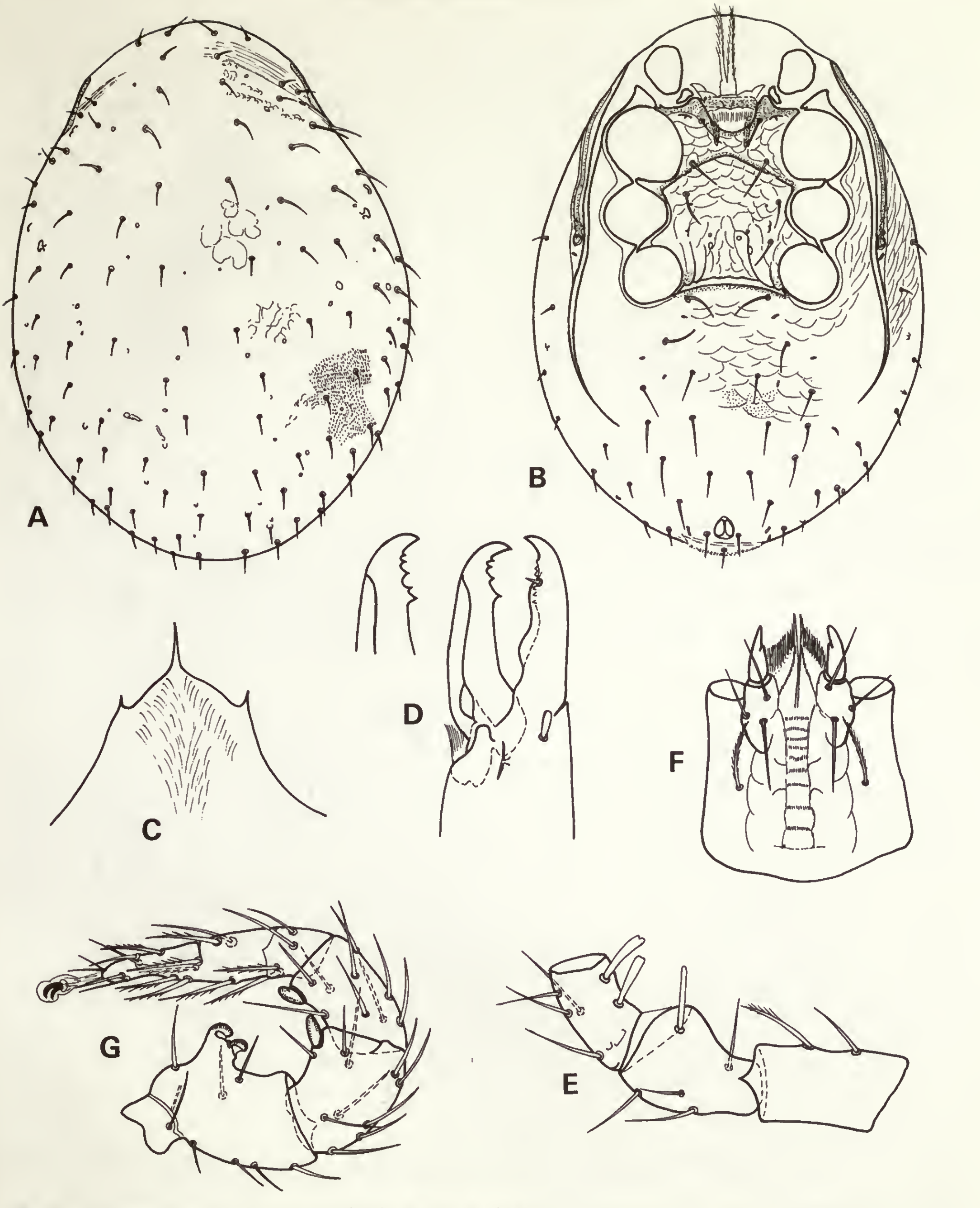

Fig. 8 *Holoparasitus inornatus* (Berlese), **male** – A dorsum, B venter, C tectum, D chelicera, E palp trochanter, femur and genu, F venter of gnathosoma, G leg II.

The tritosternum has a narrow base and pilose laciniae (Fig. 9B). The presternal shields are fused into a single narrow bar. The ventral shields are strongly reticulated and all setae are simple. The sternal shield is finely granular and is divided longitudinally at the centre. Additionally, a conspicuous procurved line passes through sternal pores II and spans the entire shield. The genital shield measures 135–160 µm long × 210–260 µm wide. Its apex is formed almost as a right

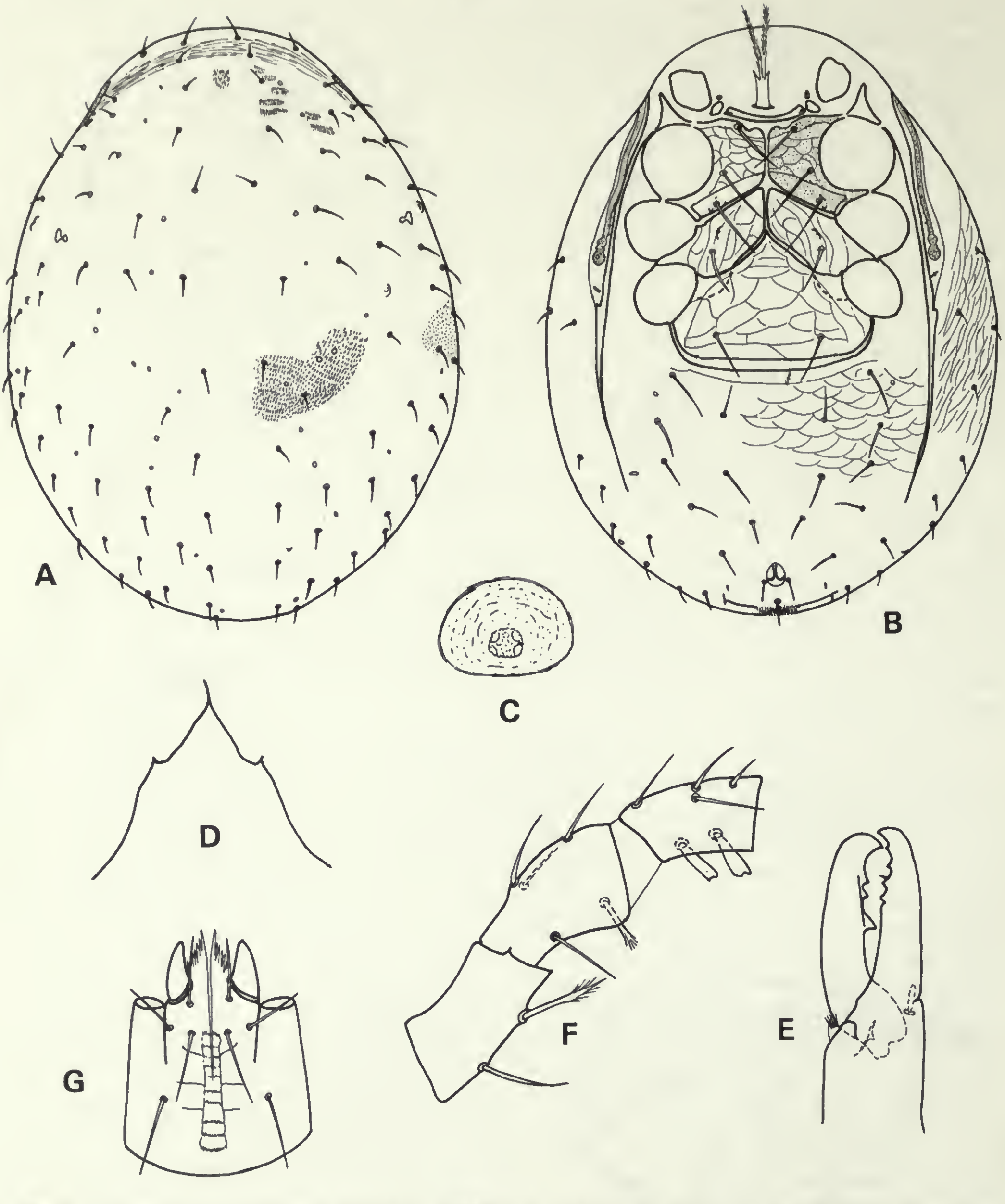

Fig. 9 *Holoparasitus inornatus* (Berlese), **female** – A dorsum, B venter, C endogynium, D tectum, E chelicera, F palp trochanter, femur and genu, G venter of gnathosoma.

angle and it does not bear an elongate tip. The endogynium appears to comprise simply an oval punctate area with a central detail (Fig. 9C). The opisthogastric region bears 8–9 pairs of simple setae. The longest of the ventral setae are the sternals which measure *c.* 65 µm and the shortest are around the posterior margin and measure *c.* 12 µm. The stigma is situated opposite the posterior margin of coxa III and the finely granular peritreme extends anteriorly to coxa I.

The tectum (Fig. 9D) has the centre portion finely tapered and it is flanked on each side by a single prong. The chelicera is shown in figure 9E. The movable digit measures 95 µm in the figured specimen and bears three teeth, one large and two smaller but of equal size. The fixed digit bears four teeth, the two distals being small, the two proximals larger. The palp trochanter, femur and genu are shown in figure 9F. The anterolateral seta on the femur is pilose distally whilst the two on the genu are spatulate. The venter of the gnathosoma is shown in figure 9G. The corniculi are strongly formed and the four pairs of gnathosomal setae are simple. Ten rows of hypognathal denticles are visible. The leg setae are slender, some on tarsi II–IV are pilose on one margin. The ambulacra are normal.

MATERIAL EXAMINED. 74 samples – 4 DNN, 85 ♂♂, 225 ♀♀.

ENGLAND: Cornwall, Devon, Dorset, Hampshire, Sussex, Kent, Hertfordshire, Gloucestershire, Suffolk, Cambridgeshire (including Huntingdonshire), Norfolk, Herefordshire, Warwickshire, Nottinghamshire, Lincolnshire, Cumbria (Westmorland), N. Yorkshire, Durham, Northumberland.

SCOTLAND: Strathclyde (Argyllshire, Mull, Ulva), Tayside (Perthshire), Highland (Inverness-shire, Ross and Cromarty), Sutherland, Shetland (Fair Isle).

WALES: West Glamorgan, Dyfed (Cardiganshire), Gwynedd (Caernarvonshire, Anglesey), Clwyd (Denbighshire).

IRELAND: Leitrim, Mayo, Sligo, Clare, Kerry.

This species is recorded mainly from mosses, litter and soil in damp habitats and is one of the two most abundant representatives of the genus in the British Isles.

DISTRIBUTION. The only previous records from the British Isles that I have been able to trace and authenticate are of specimens recorded by Halbert (1915) as *Gamasus (Ologamasus) calcaratus* (in part) from Co. Mayo and by Davis (1970) as *Holoparasitus ?inornatus* from Huntingdonshire. Davis' (*loc. cit.*) single female of *?pollicipatus* is *Holoparasitus stramenti* Karg.

It is recorded from France (Berlese, 1916), Germany (Berlese, 1906, Karg, 1971) and Switzerland (Schweizer, 1961).

Holoparasitus lawrencei sp. nov.
(Figs 10A–G, 11A–G)

MALE. The holodorsal and opisthogastric shields, which are fused ventrally posterior to coxae IV, are strongly sclerotised and completely reticulated (Figs 10A, B). The dorsum (Fig. 10A) measures 780–840 μm long × 550–610 μm wide and bears around 50 pairs of simple setae that range in length from 63 μm (*j1*) to 18 μm in the opisthonotal region. The figured specimen measures 820 μm long × 610 μm wide and bears apparently 46 setae on the left side of the dorsum and 51 on the right side. As can be seen from the figure, the setae are not entirely arranged symmetrically.

The tritosternum comprises two slender pilose laciniae that arise from below the anterior margin of the genital lamina (Fig. 10B). The sternogenital region is strongly reticulated and bears a strongly procurved line between coxae II and a similar, but less conspicuous, line between coxae III and IV. The sternogenital and median opisthogastric setae are up to 65 μm in length, whilst the three simple anal setae and the posterior ventral setae are about 20 μm long. The stigma is situated opposite the posterior margin of coxa III and the strongly granular peritreme extends to coxa I.

The tectum (Fig. 10C) is trispinate and the centre prong is long and sinuous and may be broken off. The chelicera is shown in figure 10D. The movable digit is 92 μm long in the figured specimen and bears no distinct teeth. The fixed digit bears apparently only one rudimentary tooth adjacent to the pilus dentilis. The palp trochanter, femur and genu are shown in figure 10E. The anterolateral setae of the femur and genu are spatulate, that of the genu is pilose on one margin. The venter of the gnathosoma is shown in figure 10F. The corniculi are strong and stalked, the palpcoxal setae are pilose whilst the remaining three pairs are simple, and the hypognathal groove bears about eleven rows of denticles. Leg II is shown in detail in figure 10G. The femoral apophysis is short and does not extend beyond the blunt axillary process. The ventral processes on the genu and tibia are shallow and directed anteriorly. All leg setae are slender, a number on the tarsi and tibiae of legs II–IV are stronger and pilose on one margin. The ambulacra are normal.

FEMALE. The holodorsal and opisthonotal shields, which are strongly scelerotised and completely reticulated, are fused ventrally anterior to the anus (Figs 11A, B). The dorsum (Fig. 11A) measures

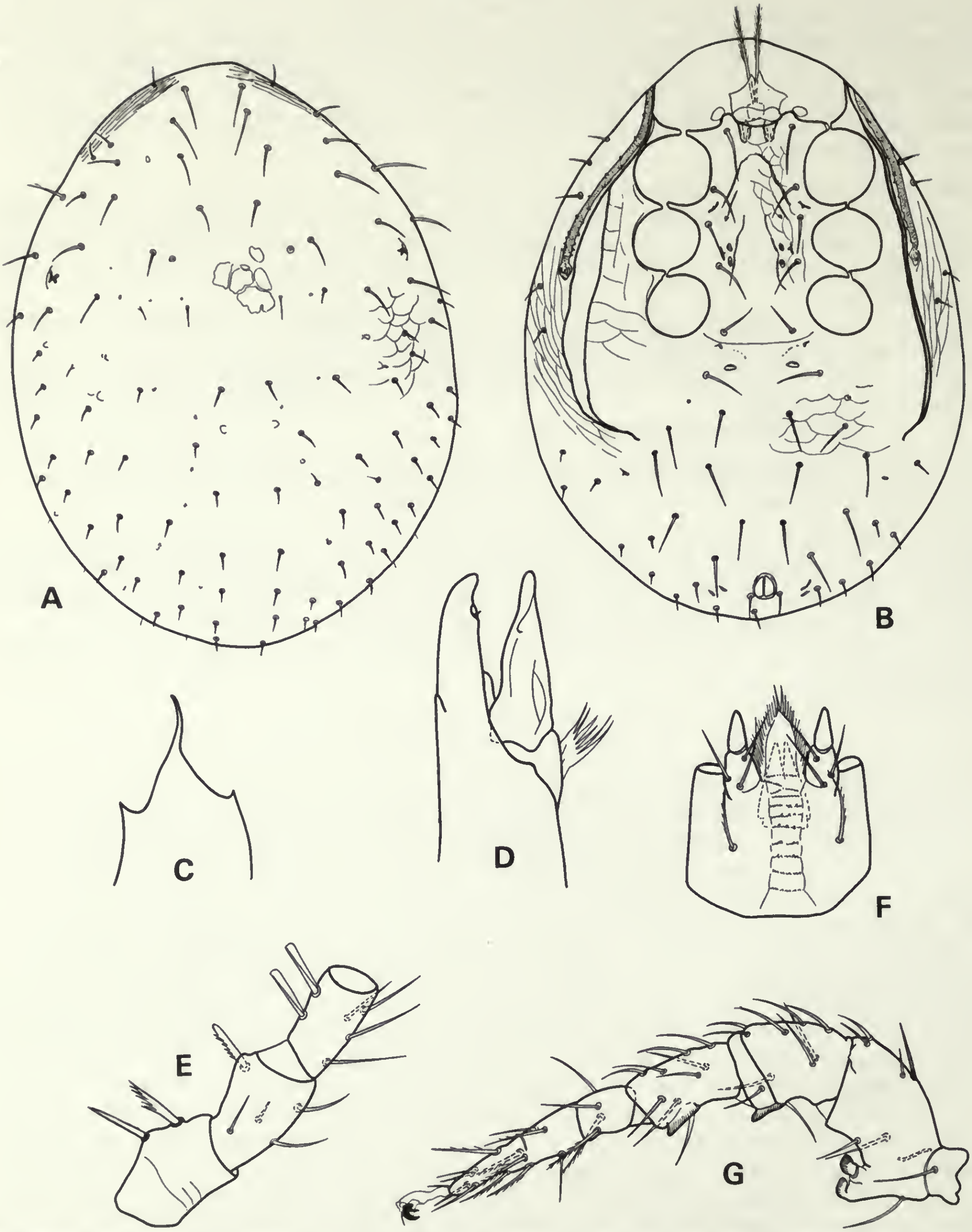

Fig. 10 *Holoparasitus lawrencei* sp. nov., **male** – A dorsum, B venter, C tectum, D chelicera, E palp trochanter, femur and genu, F venter of gnathosoma, G leg II.

850–920 µm long × 650–710 µm wide and bears up to 49 or more pairs of simple setae, about 20 pairs in the podonotal region and from 29–31 pairs in the opisthonotal region. The figured specimen – the holotype – measures 870 µm long × 660 µm wide and bears 35 setae on the podonotum, 17 on the left and 18 on the right, and 60 setae on the opisthonotum, 31 on the left and 29 on the right. The vertical setae, *j1*, and setae *j2* are the longest, measuring 50 µm or more, whilst

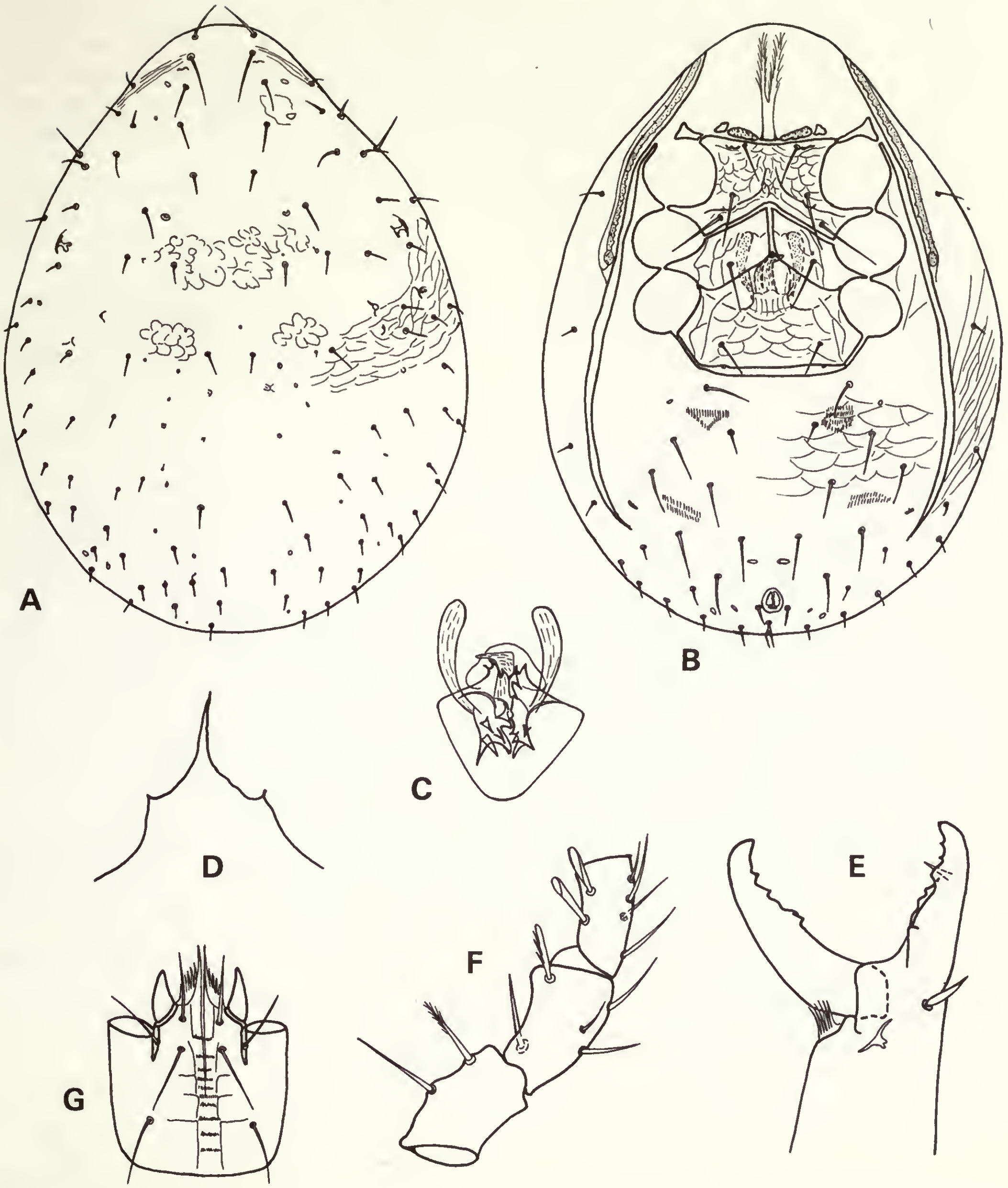

Fig. 11 *Holoparasitus lawrencei* sp. nov., **female** – A dorsum, B venter, C endogynium, D tectum, E chelicera, F palp trochanter, femur and genu, G venter of gnathosoma.

the shortest setae, the majority of those in the opisthonotal region, measure as little as 12 µm and are extremely fine.

The tritosternum (Fig. 11B) has a narrow base and pilose laciniae. The presternal shields are coarsely granular and may be entire or divided medially. The ventral shields are reticulated and all setae are simple. The sternal shield bears a pair of lines originating from the angle between coxae II and III and passing through sternal pores II and almost meeting at the centre of the shield. The genital shield measures 170–180 µm long × 265–280 µm wide. In the figured specimen – the holotype – it measures 170 µm × 280 µm. Its anterior margin is formed into slightly more than a right angle and does not have an extended tip. The endogynium is shown in figure 11C. It appears to distort easily. The opisthogastric region bears 8–10 pairs of setae. The longest of the ventral setae are probably sternal setae II, being up to 75 µm, whilst the shortest, in the opisthogastric region, measure only *c.* 12 µm. The three simple anal setae are also short. In the type the post-anal seta is bifid. The stigma is situated opposite the posterior margin of coxa III and the peritreme extends to the level of coxa I.

The tectum (Fig. 11D) is very similar to that of the male. The chelicera is as in figure 11E. The movable digit measures 125 µm in the figured specimen and bears three blunt teeth, whilst the fixed digit bears five blunt teeth. The palp trochanter, femur and genu are shown in figure 11F. The anterolateral seta of the femur is broad with one edge pectinate, whilst those of the genu are spatulate. The venter of the gnathosoma is shown in figure 11G. The setae are simple, and the hypognathal groove bears ten rows of denticles. The majority of the leg setae are fine and simple, but some of the distal setae on tarsi II–IV are pilose on one margin. The ambulacra are normal.

MATERIAL EXAMINED. 16 samples – 20 ♂♂, 16 ♀♀.

ENGLAND: **Cornwall** – Hayle, the **holotype** ♀ (1984.12.4. 1) collected by Mr P. N. Lawrence from dry, light, leaf-litter, 24.5.1975: Lelant, St Ives, 1 ♂ in a carrion trap on salt marsh and 1 ♀ in a garden trap, 1943 (Dr F. A. Turk) (these specimens not included in the type series); **Isles of Scilly** – St Agnes, 1 ♀ **paratype** (1984.12.4. 9) from litter under *Pittosporum*, 5.11.1959 (K. H. Hyatt); **Somerset** – Bath, Kennet and Avon Canal, 1♂ **paratype** (1984.12.4. 16) from moss, humus, etc., 10.3.1962 (P. N. Lawrence); **Hampshire** – Milford-on-Sea, 1 ♀ **paratype** (1984.12.4: 30) with no data (A. S. Hirst): Isle of Wight, 1 ♂ **paratype** (1984.12.4. 3) with no habitat data, April 1948 (T. A. Lloyd); **Oxfordshire** – Oxford, 1 ♂, 1 ♀ **paratypes** (1984.12.4. 17–18) from the nest of blackbird *Turdus merula*, August 1979 (Miss A. Warburton); **Norfolk** – Blackborough, 1 ♂ **paratype** (1984.12.4. 2) with no habitat data, 25.2.1969 (Miss A. Reeve); **Suffolk** – Westleton Heath, 3 ♂♂ **paratypes** (1984.12.4. 13–15) from algae on rotten wood, 7.3.1964 (P. N. and Mrs K. Lawrence); **Lincolnshire** – no locality, 1 ♀ **paratype** (1925.6.24. 584) with no habitat data, 1900 (C. F. George); **Cumbria (Lancashire)** – Grange-over-Sands, 3 ♂♂, 2 ♀♀ **paratypes** (1984.12.4. 4–8) from tree-holes, 27.1.1954 (D. Macfarlane); **Cumbria (Cumberland)** – Newton Arlosh, Carlisle, 1 ♂, 2 ♀♀ **paratypes** (1973.28) with no data (J. E. Hull).

SCOTLAND: **Tayside (Perthshire)** – Glen Farg, 2 ♂♂ **paratypes** (1984.12.4. 19–20) from mosses on deciduous trees, 24.9.1982 (K. H. Hyatt); **Dumfries and Galloway (Wigtownshire)** – Moss of Cree, 5 ♂♂, 4 ♀♀ **paratypes** (1984.12.4. 21–29) from moss in birch tree-holes, 16.9.1982 (K. H. Hyatt).

WALES: **Dyfed (Cardiganshire)** – Dol-y-Bont, 1 ♀ **paratype** (1984.12.4. 12) from damp moss, 15.8.1957 (Dr G. O. Evans).

IRELAND: **Clare** – Lough Inchiquin, 1 ♂, 1 ♀ **paratypes** (1984.12.4. 10–11) from litter near a weir, June/July 1971 (P. N. Lawrence).

This species is named after Mr P. N. Lawrence whose diligent collecting of soil arthropods has done much to increase our knowledge of the British and Irish faunas.

Holoparasitus maritimus sp. nov.
(Figs 12A–F, 13A–H, 14A–G)

Holoparasitus calcaratus: Browning, 1956: 386, Non Koch, 1839.

DEUTONYMPH. The dorsal shields are pale yellowish brown in colour, lightly sclerotised and reticulated (Fig. 12A). The podonotal shield measures 260–280 µm long × up to 480 µm wide, depending on the degree of lateral displacement of the posterior region as shown in the figure. The figured specimen bears essentially 18 pairs of setae although the left *j2* is missing. Setae *j1*, the verticals, measure *c.* 35 µm whilst the remainder reduce in length to *c.* 18 µm on the margins. The opisthonotal shield measures 190–240 µm long × 260–290 µm wide and bears 13 pairs of setae, although in the figured specimen the right *Z3* is missing. The setae range in length from 18—22 µm. The surrounding membrane bears dorsally on each side from 30–40 fine setae not exceeding 18 µm in length.

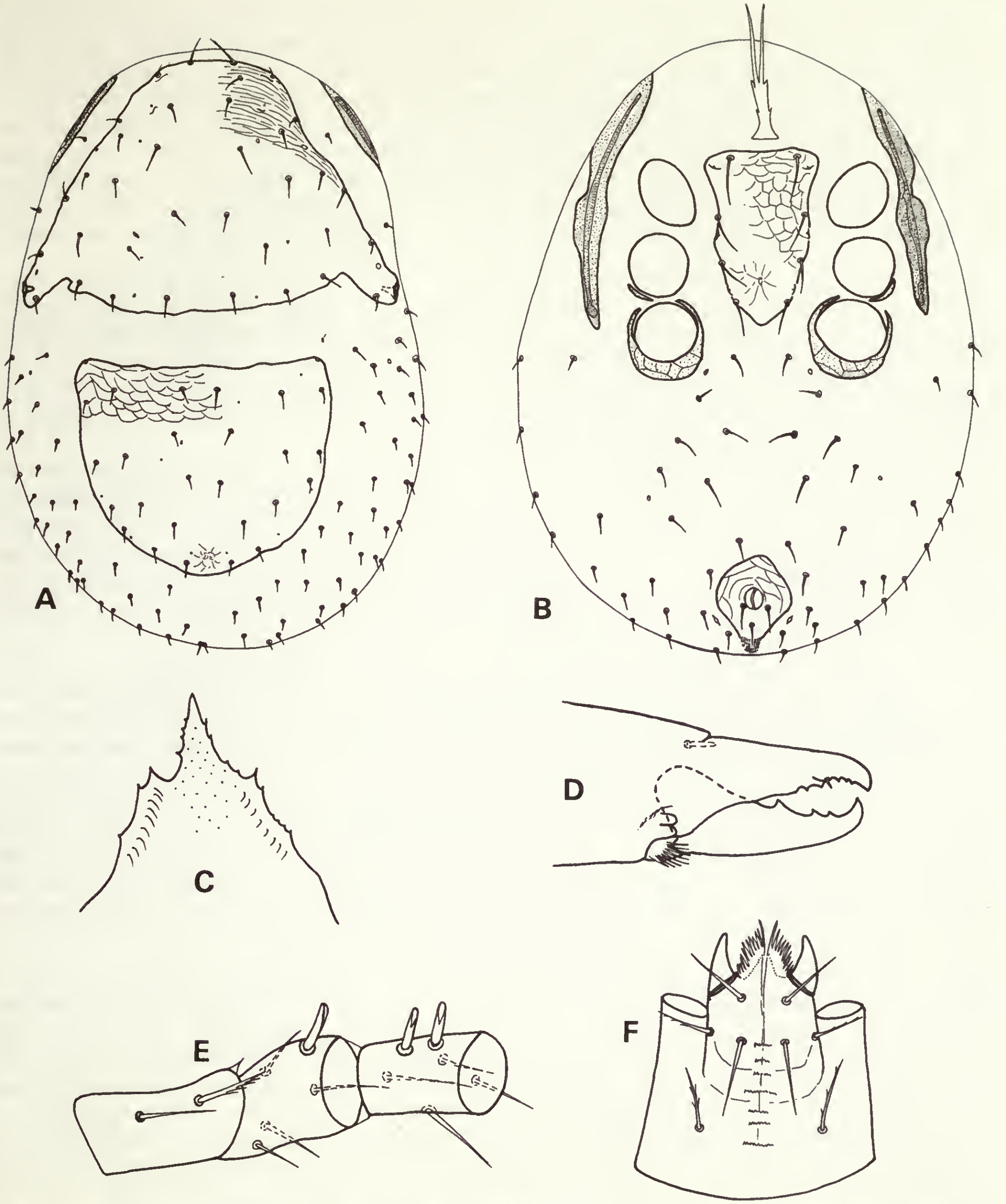

Fig. 12 *Holoparasitus maritimus* sp. nov., **deutonymph** – A dorsum, B venter, C tectum, D chelicera, E palp trochanter, femur and genu, F venter of gnathosoma.

The tritosternum has a narrow base and simple laciniae. The sternal shield (Fig. 12B) measures 160–170 μm long and is lightly sclerotised and entirely reticulated. The setae are simple. Presternal shields absent. The oval anal shield bears the usual three setae and is reticulated. The stigma is situated opposite the anterior margin of coxa IV and the granular peritreme and irregularly outlined peritrematal shield extend to coxa I. The opisthogastric setae number upwards of 16 pairs depending on the actual position of those towards the posterior margin.

The tectum (Fig. 12C) is essentially triangular and bears strong lateral teeth, but is irregularly outlined. The chelicera is shown in figure 12D. The movable digit measures 78 µm in the figured specimen and bears three widely spaced teeth. The fixed digit bears five or six smaller teeth. The palp trochanter, femur and genu are shown in figure 12E. The anterolateral setae of the femur and genu are spatulate. The corniculi and the venter of the gnathosoma are shown in figure 12F. The anterior and the internal posterior hypostomatic setae are simple whilst the external hypostomatic and the palpcoxal setae are lightly pilose on one margin. About seven rows of hypognathal denticles are present. All the leg setae are slender and the majority are simple, but a few on tarsus II are finely pilose on one margin. The ambulacra are normal, with rounded pulvilli and two claws.

MALE. The holodorsal and opisthogastric shields are fused ventrally posterior to coxae IV. They are heavily sclerotised and entirely reticulated (Figs 13A, B). The dorsum (Fig. 13A) measures 680–750 µm long × 425–500 µm wide and bears about 60 pairs of simple setae that range in length from *c.* 55 µm (setae *j1*) to 12 µm in the opisthonotal region. The figured specimen measures 730 µm long × 450 µm wide and bears apparently 60 pairs of setae on the left side and 58 pairs on the right side. The podonotal region bears 19 pairs of setae arranged symmetrically, whilst the opisthonotal region bears 41 setae on the left side and 39 on the right side.

The tritosternum comprises two slender pilose laciniae that arise from below the anterior margin of the genital lamina (Fig. 13B). The anterior margin of the sternogenital shield is moderately recessed medially. The ornamentation of the sternogenital region is without a characteristic pattern. The sternogenital setae are about 60 µm in length whilst the opisthogastric setae are shorter. The three anal setae are simple and like those in the posterior region of the opisthogastric shield measure approximately 18 µm. The stigma is situated opposite the posterior margin of coxa III and the peritreme extends anteriorly to coxa I.

The tectum is strongly granular and produced normally into a triangular process (Fig. 13C). However, in the figured specimen it is irregularly formed as shown in figure 13D. The chelicera is shown in figure 13E. The movable digit is 97 µm long and bears one large tooth and four to five small teeth. The fixed digit bears up to seven very small teeth. The palp trochanter, femur and genu are shown in figure 13F. The anterolateral seta of the femur is broad and slightly pectinate on one margin and the two anterolateral setae of the genu are spatulate. The corniculi (Fig. 13G) are stalked and are deeply cleft on their inner margins. The gnathosomal setae are all simple and there are up to 13 rows of hypognathal denticles. Leg II is shown in figure 13H. The apophysis on femur II is short, hemispherical, and does not extend beyond the tip of the swollen axillary process. The ventral processes on the genu and tibia are smooth and elongate. All leg setae are slender, some on tarsi II–IV are finely pilose on one margin. The ambulacra are normal.

FEMALE. The holodorsal and opisthonotal shields are strongly sclerotised and fused ventrally anterior to the anus (Figs 14A, B). The dorsum (Fig. 14A) is reticulated except in the median podonotal region where it is strongly granular. It measures 770–810 µm long × 520–560 µm wide and bears up to about 60 pairs of simple setae, about 20 pairs in the podonotal region and up to 40 pairs in the opisthonotal region. The figured specimen – the holotype – measures 800 µm long × 530 µm wide and bears 20 pairs of setae in the podonotal region, whilst in the opisthonotal region there are 39 setae on the left side and 34 on the right. The vertical setae, *j1*, are the longest, measuring *c.* 55 µm, whilst the remainder reduce gradually in length towards the posterior of the dorsum where the shortest are *c.* 15 µm.

The tritosternum has a narrow base and pilose laciniae (Fig. 14B). The presternal shields are fused medially and are strongly denticulate over most of their surface. The sternal shield bears a characteristic ornamentation which shows up clearly in alchohol under low magnification. There is a longitudinal median design and two pairs of liniae which form part of the reticulation. The anterior-most lines run almost diagonally from the centre of the shield towards the anterior corners, whilst the second pair runs from the centre through sternal pores II. The genital shield measures 160–165 µm long × 240–260 µm wide. In the figured specimen – the holotype – it measures 165 µm × 250 µm. Its anterior margin is almost right-angled medially and forms a short broad tip. The endogynium is shown in figure 14C and appears to distort easily. The opisthogastric

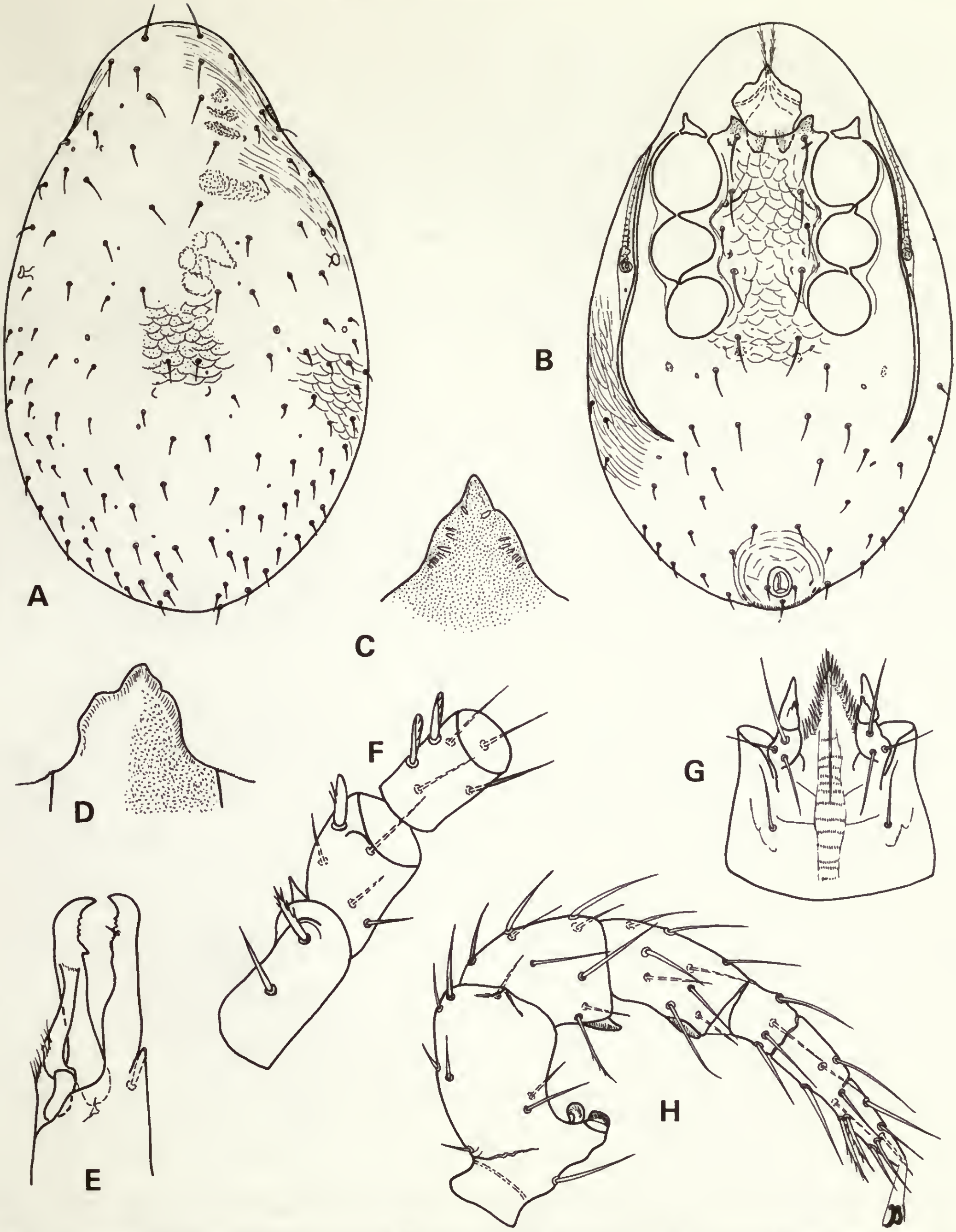

Fig. 13 *Holoparasitus maritimus* sp. nov., **male** – A dorsum, B venter, C, D tectum, E chelicera, F palp trochanter, femur and genu, G venter of gnathosoma, H leg II.

region bears 8–9 pairs of setae. The three anal setae are short (*c.* 18 µm) and similar in length to the posterior-most ventral setae. The stigma is situated opposite the posterior margin of coxa III and the peritreme extends anteriorly to coxa I.

The tectum (Fig. 14D) is granular and produced into a strong median spine and small lateral spines. The chelicera is shown in figure 14E. The movable digit measures *c.* 108 µm long and bears

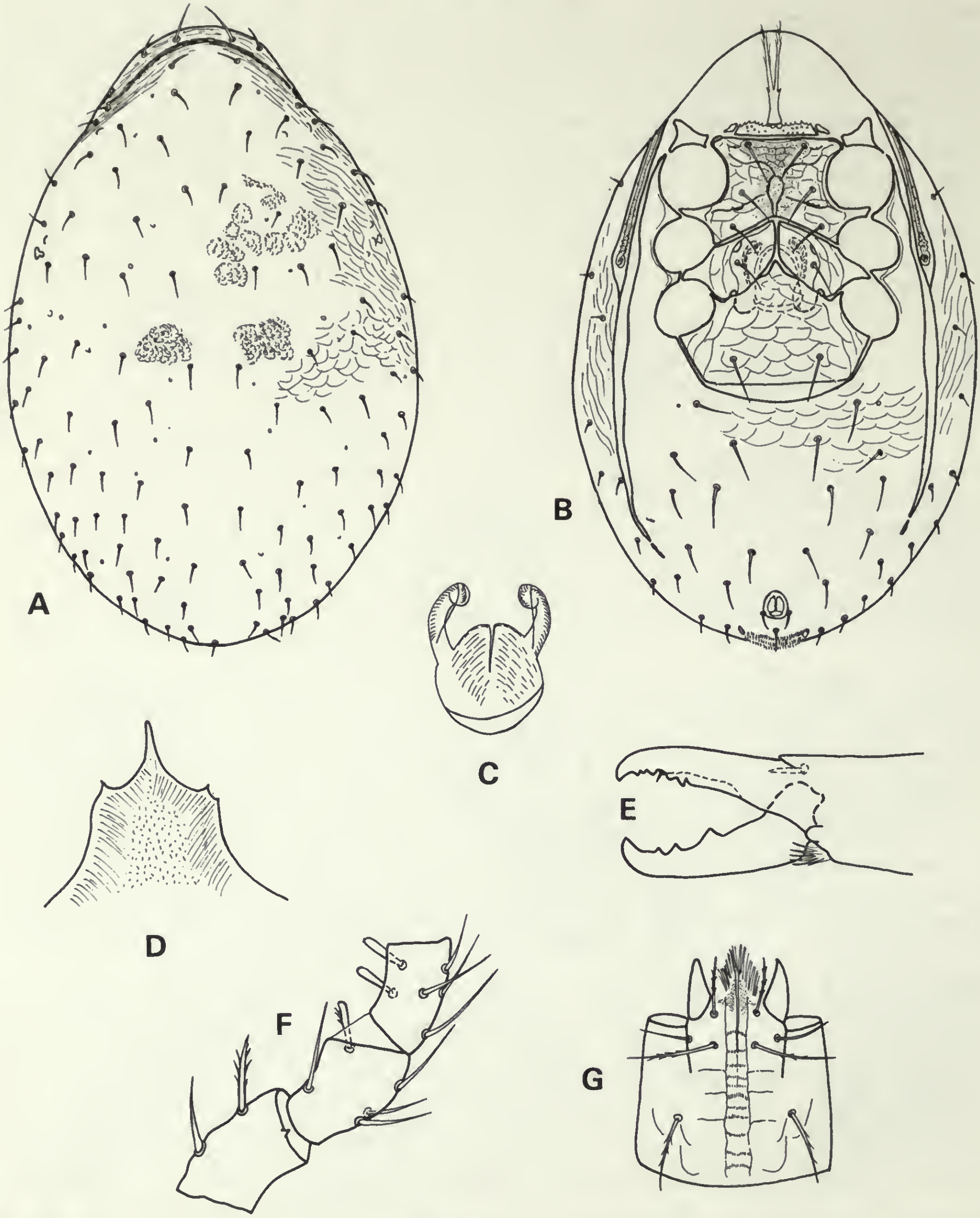

Fig. 14 *Holoparasitus maritimus* sp. nov., **female** – A dorsum, B venter, C endogynium, D tectum, E chelicera, F palp trochanter, femur and genu, G venter of gnathosoma.

three strong teeth. The fixed digit bears at least six smaller teeth. The palp trochanter, femur and genu are shown in figure 14F. The anterolateral setae on the femur and genu are spatulate, that on the femur being pilose on one margin. The venter of the gnathosoma is shown in figure 14G. The external posterior hypostomatic setae are simple, the remaining three pairs are lightly pilose. There are up to 11 rows of hypognathal denticles. The majority of the leg setae are fine and simple, but some on tarsi II–IV are pilose on one margin. The ambulacra are normal.

MATERIAL EXAMINED. 8 samples – 6 DNN, 16 ♂♂, 20 ♀♀.

ENGLAND: **Cornwall** – Kelsey Head, the **holotype** ♀ (1984.12.4. 31) and 4 DNN, 8 ♂♂, 16 ♀♀ **paratypes** (1984.12.4. 32–43) from thrift *Armeria maritima,* etc., on cliffs, 20.5.1975 (P. N. Lawrence coll.): Land's End, 1 ♀ **paratype** (1984.12.4. 46) from mossy turf, 26.5.1975 (P. N. Lawrence): Phillack, Hayle, 2 ♀♀ **paratypes** (1984.12.4. 47–48) from dried seaweed, 24.5.1975 (P. N. Lawrence): Porthleven, 2 DNN, 3 ♂♂ **paratypes** (1984.12.4. 49–53) from mossy cliff turf, 29.5.1975 (P. N. Lawrence); **Isles of Scilly** – St Agnes, 2 ♂♂ **paratypes** (1984.12.4. 44–45) from thrift and grasses on rocks by seashore, 7.4.1957 (K. H. Hyatt).

SCOTLAND: **Inner Hebrides** – Iona, 1 ♂ **paratype** (1984.12.4. 55) from sandy beach grass with *Fucus*, 3.6.1970 (P. N. Lawrence).

CHANNEL ISLANDS: **Jersey** – Elizabeth Castle, 1 ♂ **paratype** (1954.3.19. 49) from vegetation on cliff-face, 30.8.1951 (Dr G. O. Evans). This specimen was recorded by Browning (1956) as *Holoparasitus calcaratus* (C. L. Koch).

Acknowledgements

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The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as on conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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Introduction

Aulopyge is a monotypic genus represented by the species *A. huegelii* Heckel, 1841 (Fig. 1), endemic to rivers and lakes of the Yugoslavian karst regions of Dalmatia. Regrettably, there appears to be no published information on the ecology of *Aulopyge*. Populational data are lacking and the species is classified as rare (Lelek, 1980: 122).

Aulopyge possesses several unique characters (detailed below) which have led to its being placed in a separate taxonomic category, the Aulopygini (Bleeker, 1863; Karaman, 1971). In Karaman's (1971) view *Aulopyge* represents a relic of an earlier Eurasian barbine assemblage having a close relationship with the schizothoracine cyprinids—a group now confined to high-Asia. Lelek (1980: 122) simply comments '. . . it is difficult to compare it with other taxa'. Arai (1982: 146) concluded from his study of karyotypes that *Aulopyge*, which is polyploid (2n = 100), possesses a 'mosaic of barbine and gobionine characters'.

The recent acquisition by the British Museum (Natural History) of well-preserved specimens of *Aulopyge huegelii* makes possible, for the first time, a detailed anatomical study of the species. The information gained from this study has provided a basis not only for a discussion of the phylogenetic status of *Aulopyge* but also of the classification and relationships of the genus *Barbus* and other cyprinines.

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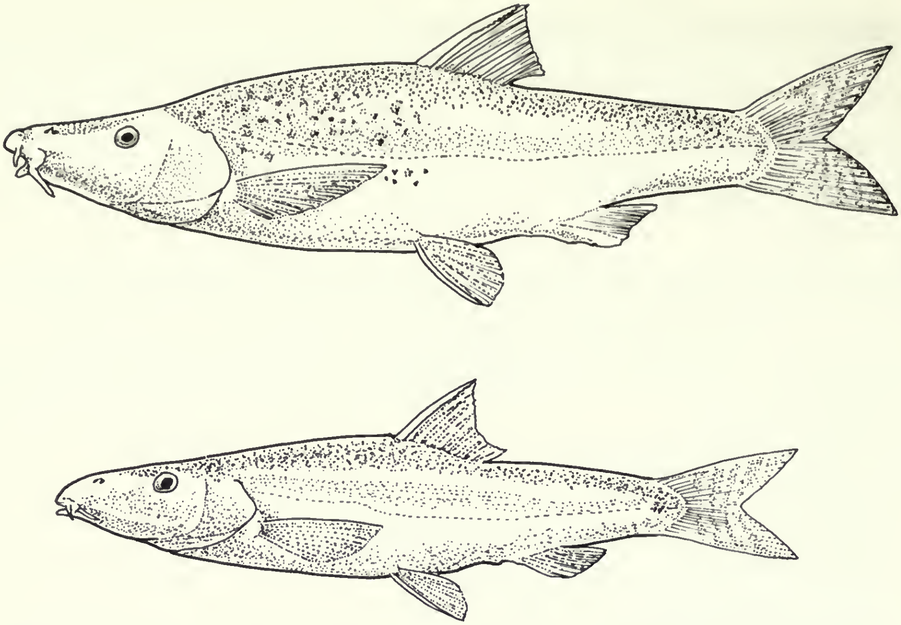

Fig. 1 *Aulopyge huegelii*, female (above) 127 mm SL and male (below) 106 mm SL.

In an earlier paper (Howes, 1981: 47–49) the classification of barbelled and non-barbelled Cyprinidae was discussed. It was reasoned that one lineage, the barbelled cyprinids, could be defined on the synapomorphic presence of paired maxillary barbels each associated with a maxillary foramen (or its suggested past presence) and a rostrally extended supraethmoid. Following the original division of the European Cyprinidae by Bonaparte (1846), the barbelled carps were recognised as the subfamily Cyprininae, while the non-barbelled taxa were ranked as the subfamily Leuciscinae. The latter group was defined simply by absence of maxillary barbels and associated nerve foramen, no synapomorphy having been discovered that would define it as a natural group.

It can be assumed from the outset therefore that *Aulopyge* belongs to the Cyprininae, since it possesses a pair of maxillary barbels supplied by a branch of the VII facial nerve. From this standpoint a more refined hypothesis of the relationship between *Aulopyge* and other cyprinids may be attempted.

Methods and materials

The osteology of *Aulopyge huegelii* was studied from an alcian-alizarin stained and a dry skeletal preparation (BMNH) 1903.12.4: 41–5), and from X-Radiographs of specimens 106, 112 and 127 mm SL (BMNH 1985.8.20: 1–3; Busko Lake, south Bosnia). Genital anatomy was studied in dissected specimens of this latter series.

Comparative osteology of a wide range of cyprinoids was studied both from alizarin stained and dry skeletal preparations. A principal data source has been the large collection of X-Radiographs of cyprinoid specimens in the BMNH. The following list is of *Barbus* specimens used in this study.

A = alizarin stained preparation; D = dissected specimen; S = dry skeleton. All catalogue numbers are BMNH.

Barbus ablabes 1983.3.30: 7–14(D), *B. albanicus* 1970.9.24: 265–67(D), *B. altianalis eduardianus* Uncat., (S), *B. a. radcliffi* 1981.4.9: 42–66(D), *B. altus* 1898.4.2: 196–205(D), *B. amphigramma* 1980.7.18: 319–332(D), *B. andrewi* 1900.11.6: 58(D), 1903.4.27: 94–95(S), *B. antinorii* (type) 1908.10.14: 7, *B. arabicus* 1976.4.7:

201–272(D), *B. argenteus* 1907.6.29: 217(S), *B.* (= *Puntius*) *arulus* 1978.8.31: 234–259(D), *B. aspilus* 1909.4.29: 74(S), *B. barbulus* 1974.2.22: 1275–77(A), *B. barbus* 1864.4.11: 41–42(D), 1908.12.28: 123(S), 1985.10.16: 62–71(A), 1985.10.16: 51, *B.* (= *Puntius*) *bimaculatus* 1981.1.21: 209–217(D), *B. binotatus* 1984.3.3: 39–60(D), 1970.9.3: 56–85(A), *B. biscarensis* 1970.3.1: 100–125(D,A), *B. bocagei* 1980.8.20: 1–6(D), *B. brachycephalus* 1899.7.25: 25–27, *B. burmanicus* 1894.5.21: 46–55(D), *B. bynni* 1861.9.9: 65(S), *B. callensis* 1951.4.10: 1–20(A,D), 1869.1.29: 4(S), *B. camptacanthus* Uncat. (S), *B. canis* 1974.2.22: 1292–94(D), Uncat., (S), *B. chola* 1935.10.18: 32–46(D), *B.* (=*Puntius*) *collingwoodi* 1892.9.2: 52–56(A), 1982.4.21: 37–38(D), *B. comiza* (syntype) 1909.7.29: 1, *B. conchonius* 1978.8.31: 21–35(D), *B. cummingi* 1978.8.31: 186–222(A), *B. dorsolineatus* 1965.3.15: 406–435(D). *B. esocinus* 1920.3.3: 80–82(D), *B. eutaenia* 1965.3.15: 93–122(D), *B.* (= *Puntius*) *filamentosus* 1981.1.21: 242–260(D), *B. fritschi* 1904.11.28: 59(S), *B. graëllsii* 1908.2.12: 21–49(D), *B. grahami* 1907.5.4: 52–57(D), *B. grypus* 1920.3.3: 1–18(D), *B. guirali* 1902.11.12: 119(S), *B. haasianus* 1976.3.18: 892–93(A), *B. harterti* 1902.7.28: 35(S), *B. holotaenia* 1984.7.5: 22–27(D), *B. holubi* 1937.10.4: 12–14(D), *B. hospes* 1980.7.18: 434–438, *B. hypsolepis* 1971.11.26: 28–41(A), *B. intermedius intermedius* 1974.1.16: 128–162(A), 166–179(D), 1902.12.13: 338(S), *intermedius australis* 1893.12.2: 36(S), *B. johnstoni* 1975.8.3: 576–80, *B. kersteni* 1978.8.3: 632–84(D), *B. ksibi* 1934.10.25: 1–14(D), *B. leonensis* 1974.9.18: 77–177(A), *B. lineomaculatus* 1974.1.16: 396–411(D), *B. litamba* 1974.1.11: 88–93(D), *B. lithopides* 1889.2.1: 559–61(D), *B. longiceps* 1936.4.6: 5–11, 1949.9.16: 90–92, 1864.8.20: 21(S), *B. luteus* 1874.4.28: 23(S), 1968.12.13: 201–212(D), *B. macrolepis* 1972.11.28: 9–12(D), *B. macrops* 1960.6.7: 111–160(D), *B. mattozi* 1962.8.22: 2–6(D), *B. meridionalis* 1935.10.28: 14–17(D,S), *B. minimus* 1974.1.16: 276–292(D), *B. mursa* 1872.5.30: 67–68, *B. nasus* 1902.1.4: 22(S), *B. natalensis* 1862.8.28: 8(S), *B. neglectus* 1980.7.10: 1–26(D), *B. neumayeri* 1969.3.6: 31–50(D), *B.* (= *Puntius*) *orphoides* 1974.10.10: 865–872(D), *B. oxyrhynchus* 1893.12.2: 31(D), 1906.8.25: 17(S), *B. paludinosus* 1979.3.1: 1–53(D), 1908.1.20: 84(S), cf. *paludinosus* Uncat., (A), *B. paytoni* 1976.2.2: 29–31(D), *B.* (= *Puntius*) *pentazona* 1954.11.23 7–82(A), *B. perince* 1907.12.2: 1268–77(D), *B. plebejus plebejus* 1887.4.5: 15–16, 1982.2.24: 149–155(D), *plebejus peloponnesius* 1964.6.12: 20–26(D), *B. poechi* 1962.7.5: 4–15(D), *B. progenys* 1903.7.28: 155(S), *B. profundus* 1970.5.14: 19–30(D), *B.* (= *Tor*) *putitora* 1884.2.1: 52(S), *B. radiatus* 1982.4.13: 4597–4605(D), *B. reinii* 1903.10.29: 10(S), *B. rocadasi* 1911.6.1: 26(S), *B. rothschildi* 1902.7.28: 22–26(D), *B.* (= *Puntius*) *sarana* 1933.8.19: 7–14(D), *B. schejch* 1931.12.21: 4(D), *B. sclateri* (syntypes) 1861.11.20: 9–13, *B. serra* 1937.10.4: 6–11(D,S), *B. setivemensis* 1905.11.28: 59(S), *B. sharpeyi* 1920.3.3: 71–75(D), *B.* (= *Puntius*) *sophore* 1889.2.1: 777–782(D), *B. subquincunciatus* 1934.10.29: 1(D), *B.* (=*Tor*) *tambroides* 1982.4.21: 39(D), *B. tenuis* 1975.12.29: 250–265(D), *B. thalamakanensis* 1976.3.18: 363–550(D), *B.* (=*Puntius*) *titteya* 1974.6.11: 8–12(A), *B.* (=*Tor*)*tor* 1893.6.30: 31–38(D), *B. trimaculatus* 1907.4.9: 98(S), *B. tropidolepis* 1936.6.15: 599–629(A), *B. xanthopterus* 1973.5.21: 198(D).

Species without a suffix and those cited in the text but not listed above have been examined by X-Radiography only.

Nomenclature

Because the concept of cyprinid subfamilies and other higher categories used here differs from that of previous authors (see Discussion) I have adopted the following nomenclature.

Subfamily Cyprininae (cyprinines): a monophyletic assemblage (see text) which includes the following subgroups:

*barbins: a possibly monophyletic group, the members of which possess a foraminate dilatator fossa (see text and Table 3 for included taxa). This group embraces, in part, the Barbinae and Barbini of previous authors.

*labeins: a monophyletic group *sensu* Reid, 1982 and 1985; includes Labeinae, Labeini, Labeoinae and Garrini of previous authors.

*squaliobarbins: a monophyletic group *sensu* Howes, 1981.

*schizothoracins: a supposed monophyletic group (see text); the Schizothoracinae and Schizothoracini of previous authors.

*other cyprinines: an unresolved assemblage of taxa not included in any of the above categories and lacking a foraminate dilatator fossa (see text and Table 3).

Subfamily Leuciscinae (leuciscines): a possibly non-monophyletic assemblage including Abraminae, Cultrinae etc. of previous authors.

After this paper had been submitted for refereeing, my attention was drawn to a publication by Chen *et al.* (1984). These authors have proposed an hypothesis of cyprinoid relationships whereby they recognise the Cyprinidae as comprising two 'series', the Barbini and Leuciscini. They further recognise two monophyletic groups (tribes) within the Barbini, *viz.* Barbines and Tincanes, of which the Tincanae, Cyprininae, Barbinae and Labeoninae (*sic*) are the constituent lineages. My concept of Cyprininae corresponds to Chen *et al.* 'Barbini', whilst my subgroups embrace their subfamilies.

The appellations 'small' and 'large' are often given to African *Barbus* species. As used here, 'small' refers to those species in which the striae on the exposed part of the scale are radiate, the fish usually less than 150 mm SL adult size, and the body often marked with spots or lateral stripes; 'large' refers to those species in which the scale striae are more or less parallel, the fish more than 150 mm SL adult size, and the body lacking any noticeable markings.

Abbreviations used in the figures

aa	anguloarticular
abr 1	1st branched anal fin ray
afsl-3	anal fin rays (unbranched)
ah	anterohyal
asn	anterior supraneural
at	anal tube
bb	basibranchials
bh	basihyal
bo	basioccipital
bp	basioccipital process
bsr	branchiostegal ray
cb	ceratobranchials
ccf	coracoid-cleithral foramen
cl	cleithrum
cor	coracoid
csi	cavum sinus imparis
ct	connective tissue
de	dentary
df	dilatator fossa
dfo	dilatator foramen
dfs	dorsal fin rays
dh	dorsohyal
eb	epibranchials
ect	ectopterygoid
enf	ectopterygoid facet
ent	entopterygoid
epf	entopterygoid-palatine facet
ep	epural
epo	epioccipital
fc	frontal canal
fm	foramen magnum
fr	frontal
frl	frontal lamina
hb	hypobranchial
hmf	hymandibular fossa
hs	haemal spine
hyo	hyomandibula
hyp	hypurals
hys	hypurapophysis
ic	intercalar
ih	interhyal
int	intestine
io	infraorbitals
iop	interoperculum
ip	infrapharyngobranchials
lac	lachrymal
lct	lachrymal canal tube
le	lateral ethmoid
lef	lateral ethmoid facet
llen	lateral ethmoid-entopterygoid ligament
loc	lateral occipital fenestra
me	mesethmoid
met	metapterygoid
mp	masticatory plate of basioccipital
nc	neural complex
nca	neural canal
ns4	neural spine of 4th centrum
$nspu_2$	neural spines of 2nd preural centrum
op	operculum
os	orbitosphenoid
ov	oviduct
pa	parietal
pc	parietal canal
pcl	postcleithrum
pe	preethmoid
ph	posterohyal
phy	parhypural
po	preoperculum
poc	preopercular canal (bone enclosed)
pro	prootic
ps	parasphenoid
pte	pterotic
pts	pterosphenoid
ptt	posttemporal
qf	quadrate facet
ra	retroarticular
rp	proximal radials
sb	splenial bone
scc	subcutaneous canal
scp	scapula
se	supraethmoid
so	supraoccipital
sop	suboperculum
sor	supraorbital
sp	sphenotic
spr	sphenotic process
srp	supraethmoid rostral process
sy	symplectic
vh	ventrohyal
vo	vomer
I	olfactory nerve foramen
II	optic fenestra
V	trigeminal nerve foramen
VII	facial nerve foramen
IX	glossopharyngeal nerve foramen
X	vagus nerve foramen

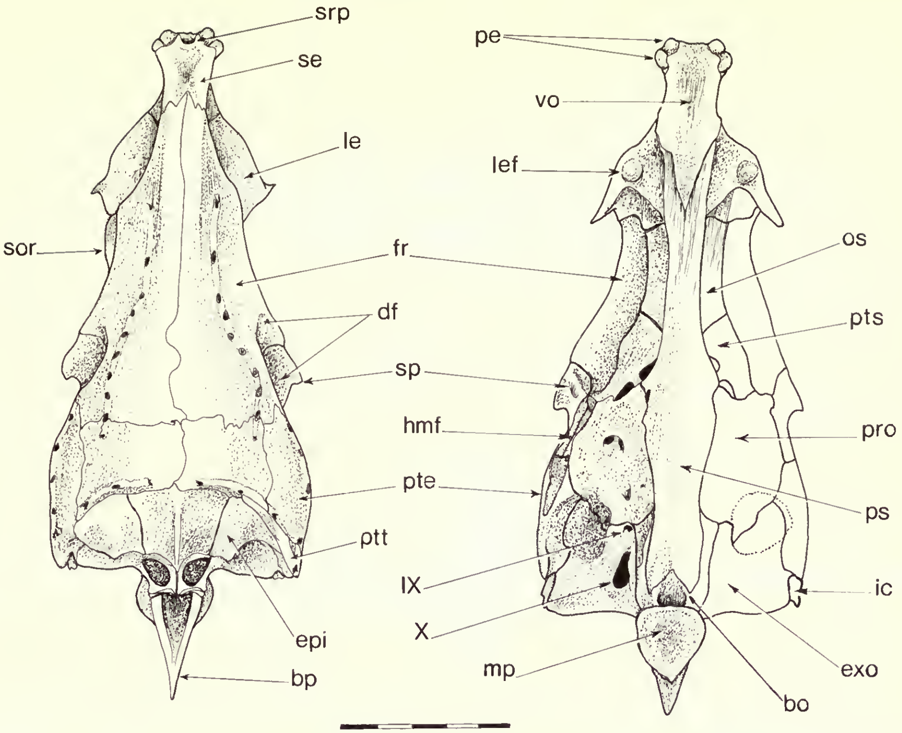

Fig. 2 *Aulopyge huegelii,* neurocranium in dorsal (left) and ventral (right) views. Scale bar in mm.

Anatomical characters in *Aulopyge* and their phylogenetic significance

The cranium of *Aulopyge* is shown in Figs 2 and 3. In general appearance it is depressed and elongate. The ethmoid region is narrow and shallow, the supraethmoid bearing a sloped, valley-like depression and anteriorly having slight lateral expansions and a short rostral extension which is medially indented (srp, Fig. 2). The kinethmoid (Fig. 4d) is of the rod-shaped type considered by Howes (1978; 1981) as plesiomorphic for cyprinoids. Each lateral ethmoid is extended medially along the parasphenoid and contacts its partner, their being no anterior myodome. Laterally, each bone extends a narrow, posteriorly pointing wing which ventrally bears a well-developed round facet against which the entopterygoid facet articulates (lef, Fig. 2). This is an unusual feature and is discussed further below.

The frontals are narrowed anteriorly and nasal bones are absent; the supraorbital bones are small but not excessively reduced. Otherwise, the cranium of *Aulopyge* exhibits no features which may be regarded as anything but plesiomorphic among cyprinoids, *viz.*: the prootic is elongate with a long lateral commissure, the subtemporal fossa is round and deep, there is no posttemporal fossa, and the basioccipital has a short posterior process and small, round masticatory plate (Figs 2 & 3).

Likewise the jaws and elements of the suspensorium (Fig. 4), other than the entopterygoid (discussed below), show no departure from the 'generalised' cyprinoid morphology (see Howes, 1978, 1981, 1984).

The lateral ethmoid and its articulation with the entopterygoid

The presence in *Aulopyge* of a facet, ventrally on the lateral ethmoid, apposing an entopterygoid facet is a feature which has a restricted distribution amongst the Cyprinidae. Ramaswami (1955) drew attention to a mesial entopterygoid facet articulating with the lateral ethmoid in *Labeo*

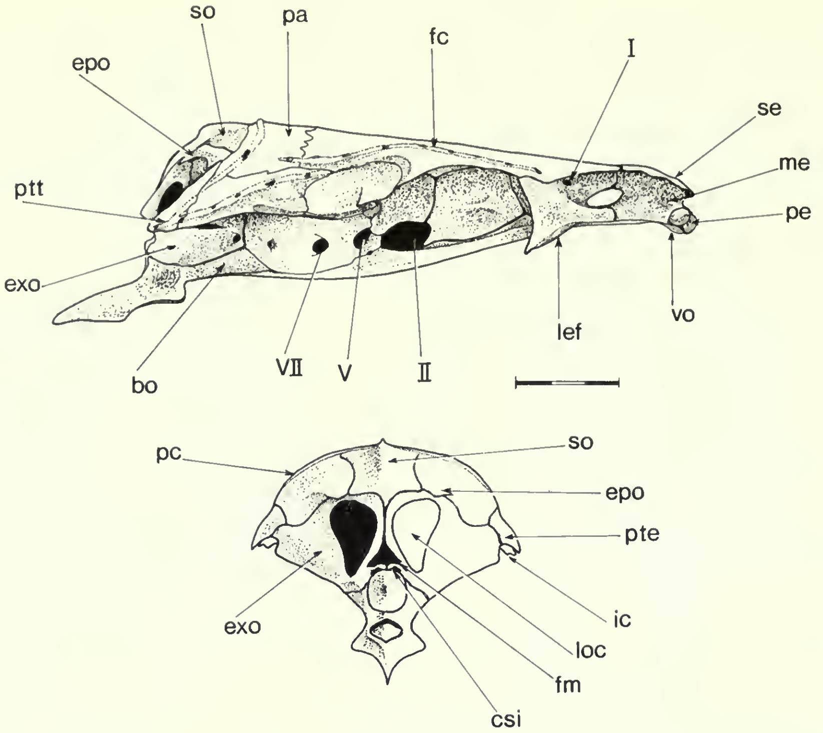

Fig. 3 *Aulopyge huegelii*, neurocranium in lateral (above) and posterior (below) views. Scale bar in mm.

macrostoma and *Cyprinus carpio*. Howes (1976: 46) noted that such a facet was variously developed in cyprinids, supposing it best developed in those species with a long ethmoid region and least in those with a short ethmoid. However, further investigation has not endorsed this claim and it appears that the presence of an entopterygoid facet is not positively correlated with the length of the ethmoid. Its presence seems to require a purely phylogenetic rather than a functional explanation. Thus, entopterygoid-lateral ethmoid facets occur only in taxa included in the Cyprininae, being absent, but for a single exception (*Tinca*; see below), in the Leuciscinae, (i.e. all non-barbelled cyprinids). The most highly developed form of this articulation occurs in some species of *Barbus*, *Cyprinus* and in the schizothoracin genus *Diptychus* (Figs 5 & 6).

In *Cyprinus*, the ventral surface of the lateral ethmoid wing is broadly triangular with the ventral articular facet situated antero-medially (Fig. 5b); the facet is sloped posteriorly and articulates against a round facet on the dorso-anterior border of the entopterygoid, just posterior to that bone's articulation with the palatine.

In *Barbus barbus*, *B. nasus*, *B. plebejus*, *B. bocagei*, *B. meridionalis* and *B. barbulus* the lateral ethmoid facet is a large triangular platform (Fig. 5a). In some 'large' *Barbus* species, e.g. the Asian, *B. grahami*, *Barbus* (= *Tor*) *tor* and the North African, *B. setivemensis* the articular, boss-like facet is situated at the midpoint of the lateral ethmoid wing (Figs 6c–e). In all these species the entopterygoid facet is moderately developed. In yet other African and Asian 'large' *Barbus* species the lateral ethmoid facet lies along the posterior margin of the wing and in some taxa, e.g. the majority of 'large' African *Barbus* and *Varicorhinus* species, a distinct facet is barely developed, there being only a bevelling of the posterior border of the wing (Figs 5d & 6f). In these taxa an entopterygoid articulatory surface is feebly developed also (Fig. 5d). However, in the majority of African and Asian *Barbus* examined lateral ethmoid and entopterygoid facets are lacking. This appears to be the condition in all the so-called 'small' African *Barbus* species.

Amongst schizothoracins a lateral ethmoid facet is variously developed (Figs 6k–m), but in

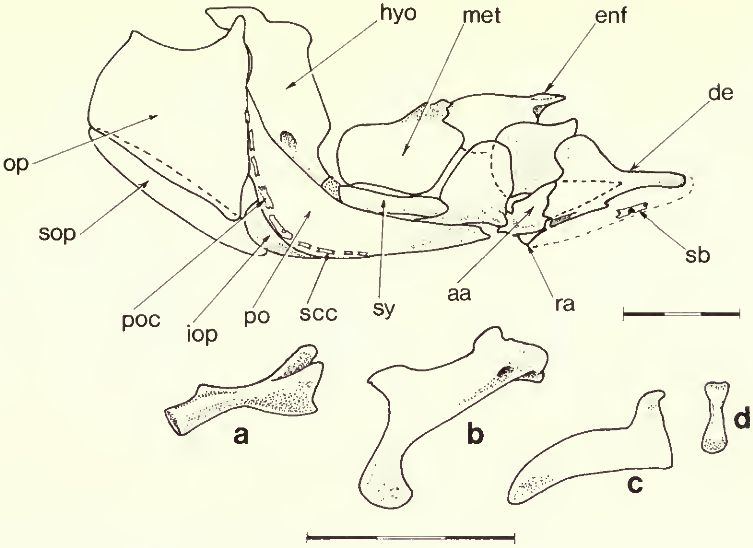
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Fig. 4 *Aulopyge huegelii.* (Above) suspensorium in lateral view; (below), (a) palatine; (b) maxilla; (c) premaxilla; (d) kinethmoid. Scale bar in mm.

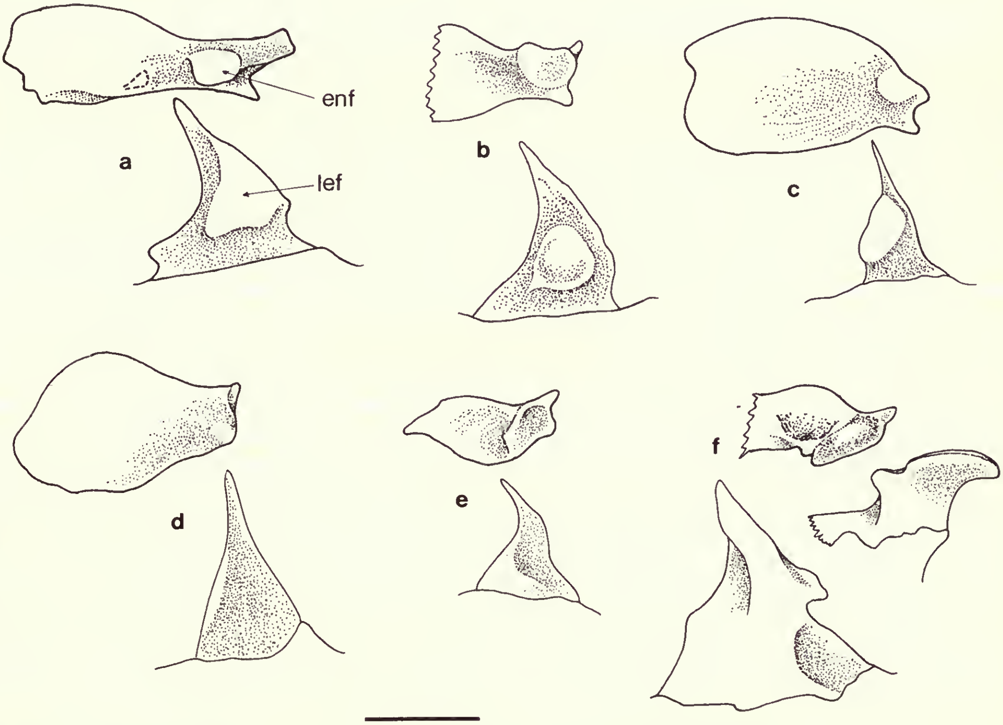
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Fig. 5 Articular facets on the ventral surface of the lateral ethmoid wing and antero-dorsal surface of the entopterygoid in: (a) *Barbus barbus*; (b) *Cyprinus carpio*; (c) *Tor putitora*; (d) *Barbus oxyrhynchus*; (e) *Tinca tinca*; (f) *Labeo coubie*, entopterygoid facet also shown in lateral view. In (a) dashed outline represents attachment area of lateral ethmoid ligament. Anterior to the left. Scale bar = 5 mm.

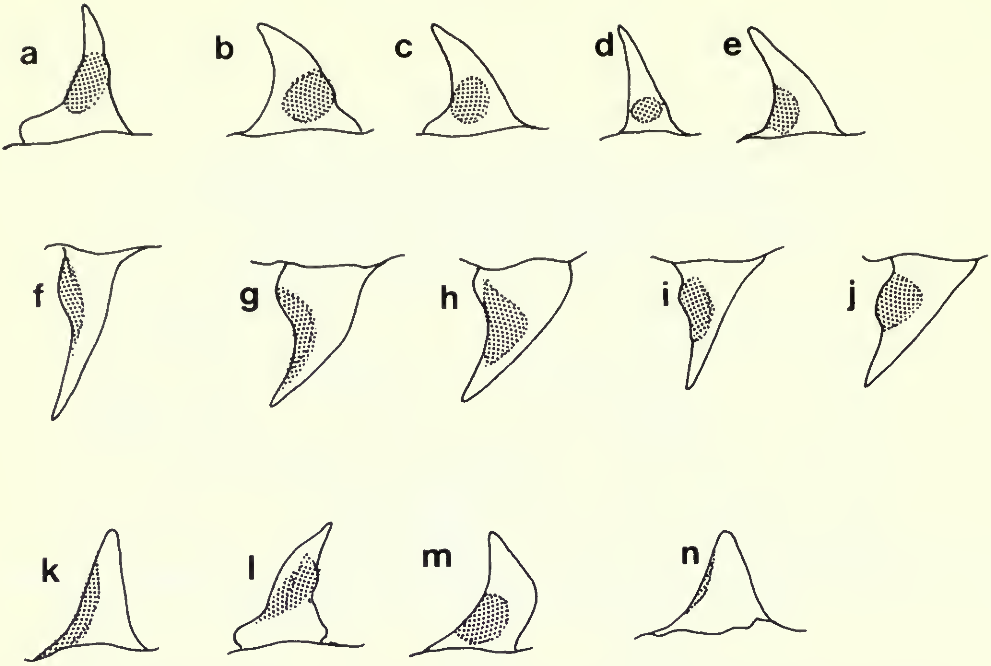

Fig. 6 Lateral ethmoid facets of: (a) *Diptychus dybowski*; (b) *Barbus nasus*; (c) *B. grahami*; (d) *B. setivemensis*; (e) *B. lithopides*; (f) *Varicorhinus tanganicae*; (g) *Barbus callensis*; (h) *B. serra*; (i) *B. progenys*; (j) *B. canis*; (k) *Schizothorax grahami*; (l) *S. taliensis*; (m) *S. intermedius*; (n) *S. esocinus* and *S. richardsoni*. Semi-diagrammatic; all drawn to same scale; anterior to the left.

none, apart from *Diptychus* (Fig. 6a) is there a condition approaching that in the Eurasian *Barbus* species cited above, and an entopterygoid facet is rarely present.

In the squaliobarbins (*Squaliobarbus, Ctenopharyngodon* and *Mylopharyngodon*), a group considered as primitive cyprinines (see Howes, 1981, and Fig. 21), the lateral ethmoid articular surface is elongate, with a bevelled anterior margin against which abuts the posterior edge of the palatine. The entopterygoid articulates only with the posterior rim of the lateral ethmoid wing as in some 'large' African *Barbus* described above.

In labeins, *Labeo* (*sensu* Reid, 1985) has an extensive lateral ethmoid whose ventral surface bears a fossa which cups an entopterygoid condyle (Fig. 5f). *Garra*, on the other hand, has a narrow lateral ethmoid wing, which is only connected ligamentously with the entopterygoid.

Lateral ethmoid and entopterygoid facets are also lacking in *Cyprinion, Gibelion* and *Capoeta*; whether this condition represents secondary loss or a plesiomorphic state is uncertain in the absence of recognised synapomorphies indicating the relationships of these taxa.

That there is a phylogenetic rather than a functional basis for the various types of articulatory surfaces among cyprinines is seemingly supported by the following observations.

In those taxa where there is a well-developed articulation between the two bones, e.g. *Cyprinus* and some Eurasian *Barbus* species, the anterior portion of the entopterygoid is almost horizontal (Figs 8a & b), and it is also horizontal in those taxa which have only a moderate articulation between these bones, e.g. some 'large' African *Barbus* and *Varicornhinus* species (Fig. 8c). In *Aulopyge*, where there are well-developed lateral ethmoid and entopterygoid facets, the entopterygoid slopes at an angle similar to that in taxa which lack such close articulation, e.g. *Schizothorax esocinus* (Fig. 8d). Thus, whilst the slope of the entopterygoid is correlated with cranial width (being horizontal in those taxa with the widest crania) there is apparently no correlation between slope (both in the horizontal and vertical planes) and the presence or absence of

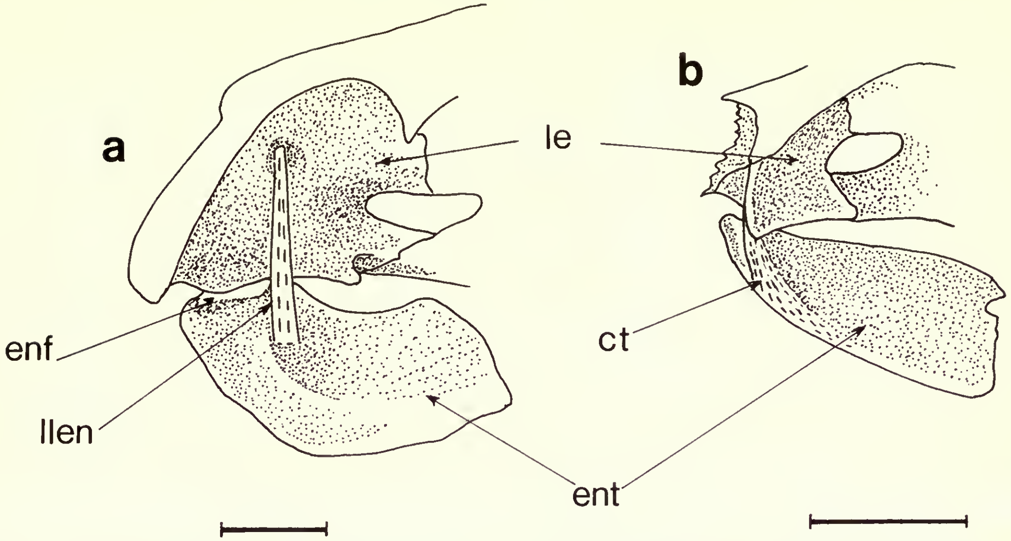

Fig. 7 Connection between the lateral ethmoid and entopterygoid in, (a) Cyprininae; *Barbus barbus*, and (b) Leuciscinae; *Raiamas loati*. Scale bars = 3 mm.

articulatory surfaces. Even if one accepts this as evidence for the apomorphic status of articulatory facets, there is nothing to suggest which type of facet morphology is the more derived, be the extensive well-developed articulation of the Eurasian *Barbus* and *Cyprinus* or the less intimate connection of the African *Barbus* and *Varicorhinus* species.

It was noted above that all but one leuciscine taxon lack an articular connection between the lateral ethmoid and entopterygoid. Instead, the two bones are ligamentously connected and often the entopterygoid extends anterior to the lateral ethmoid (Fig. 7b). *Tinca* is the exception amongst leuciscines, in that the entopterygoid bears a distinct and deep fossa which articulates with a lateral ethmoid facet (Fig. 5e).

That articulatory lateral ethmoid and entopterygoid facets occur only amongst cyprinines further supports an internal division of the Cyprinidae, but whether this represents the derived condition, and if so, whether it is synapomorphic for those taxa in which the articulation occurs is problematic (see remarks above).

The types of ligamentous connection between the lateral ethmoid and the entopterygoid support the subfamilial division of the Cyprinidae (see p. 166 and Appendix 2). The widespread ostariophysan condition is for there to be a strong ligament running from the upper medial face of the lateral ethmoid wing to the dorsolateral surface of the entopterygoid (Fig. 7a; see also Vanderwalle, 1977, Fig. 4 of *Barbus barbus*).

In all members of the subfamily Cyprininae investigated, apart from *Ctenopharyngodon*, there is a single, slender ligament connecting the bones; in *Ctenopharyngodon* a broad ligamentous band connects the bones. In the subfamily Leuciscinae a ligament of the type found in the Cyprininae is absent and connection between the lateral ethmoid and entopterygoid is *via* undifferentiated connective tissue. Vandewalle (1977) showed in *Leuciscus leuciscus* a ligament (labelled Li18) running from the edge of the lateral ethmoid to the entopterygoid. I find no such discrete ligament, but instead thickened connective tissue running to the lateral edge of the entopterygoid (Fig. 7b).

The widespread occurrence and constant position of the lateral ethmoid-entopterygoid ligament amongst ostariophysans suggests it is plesiomorphic and thus its absence in the Leuciscinae is considered a derived loss. It is interesting to note in this group, as compared with the Cyprininae, what appears to be an anterior shift of the entopterygoid head, and its somewhat looser connection with the palatine, features which may be associated with the absence of a ligamentous connection.

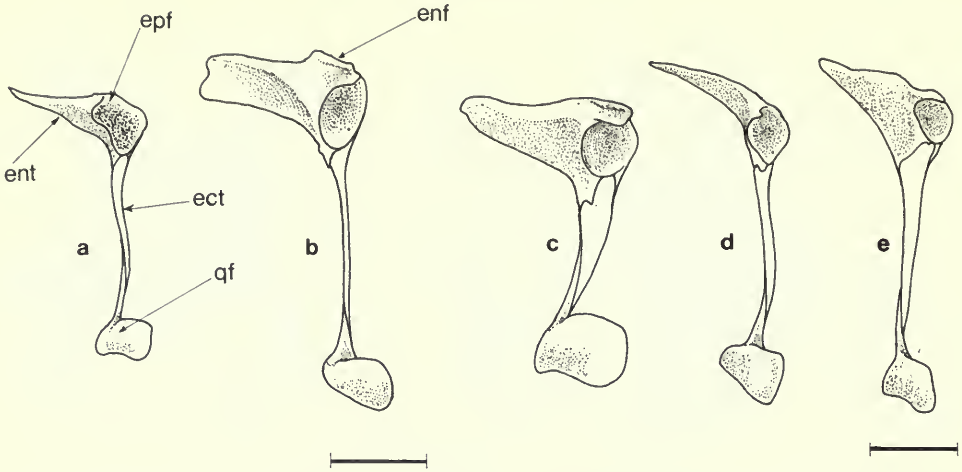

Fig. 8 Anterior views of the right suspensorium in; (a) *Cyprinus carpio*; (b) *Barbus barbus*; (c) *Varicorhinus tanganicae*; (d) *Schizothorax esocinus*; (e) *Aulopyge huegelii*. Scale bar for a–d = 5 mm, for e = 1 mm.

Sensory canals and their associated bones

Aulopyge possesses the pattern of supraorbital canals corresponding to Illick's (1956) group IVAA, where a marked gap separates the supraorbital and infraorbital canal systems; the frontal and parietal canals are distant and the parietal canals are separated from one another by a midline gap. The dorso-cranial canals are bony tubes lying on the surface of their respective bones; the frontal canal contains 9–10 pores. The infraorbital series is reduced to bony tubes, the first and last infraorbitals being fragmented into several elements (Fig. 9a).

The most unusual feature of the *Aulopyge* infraorbital canal is its disassociation from the lachrymal (1st infraorbital, lac, Fig. 9a). In an alizarin stained specimen of 52 mm, the weakly ossified canal lies somewhat ventral to the well-developed elongate 'lachrymal' bone. This situation is evident in all the specimens of *Aulopyge* examined (60–127 mm SL) with the exception of an 84 mm SL female, where a bony canal tube is attached to the face of the lachrymal (Fig. 9b). Those portions of the canal posterior and anterior are epidermal.

The mandibular-preopercular canal is incomplete. Only a single, small tube lies below and separate from the dentary (Fig. 4). There is a short groove along the ventro-lateral border of the dentary, but no sign of a canal associated with the anguloarticular. The canal reappears as a series of weakly ossified, epidermal tubes along the posterior part of the preoperculum; at the point of curvature, the canal runs through the bone (poc, Fig. 4), then continues in three or four epidermal tubes, the last terminating close to the dorsal tip of the preoperculum.

The development of cyprinoid sensory canals was studied by Lekander (1949) who summarised the results and theories of previous authors. Lekander showed that the sensory canals can, from the earliest ontogenetic stages either be united with their respective bone, later fuse with it, or remain separate from it. He drew particular attention to the 'antorbital' (= lachrymal of most authors) noting that in some cypriniforms, the canal remains separate from its lamellar portion. Such is the case in the Cobitidae, where there is apparently an antorbital, i.e. a bone lying antero-dorsal to the 1st infraorbital, while the elongate lachrymal is by-passed ventro-laterally by the subcutaneous sensory canal (Lekander, 1949; Parshall, 1983).

As in the adult *Aulopyge*, the developing infraorbital canals in some cyprinids often appear irregularly spaced and remain unfused to one another; a 'splenial' bone may be present (Lekander, 1949: 81), and the preopercular latero-sensory canal tubes remain separated from one another and from the preoperculum (Lekander, 1949: 95; 102; 112).

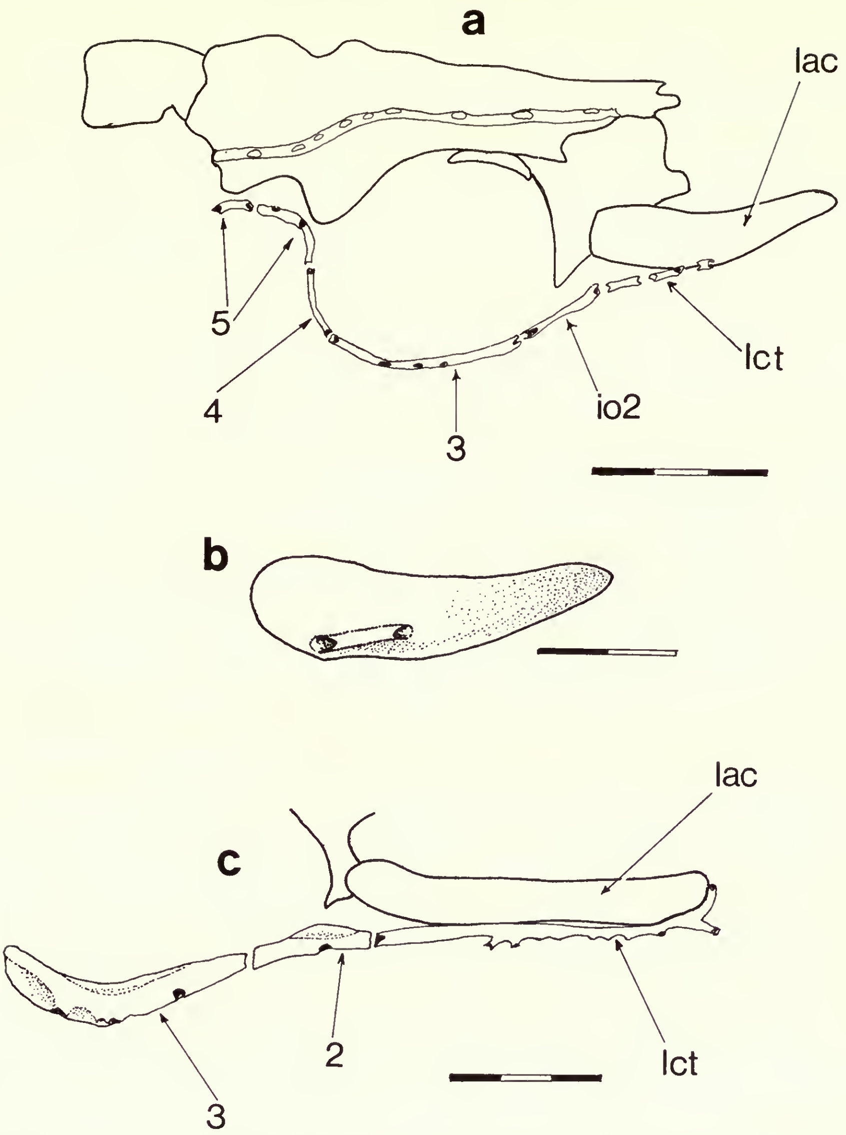

Fig. 9 Infraorbital bones of *Aulopyge huegelii*; (a) complete series of 52 mm SL specimen; (b) the lachrymal of an 84 mm SL specimen with canal attached to the bone. (c) *Barbus barbulus*, showing disassociated lachrymal canal. Scale bars in mm.

Lekander (1949: 113) makes the point that sensory canals in cyprinids develop later than in most other teleosts he examined. Whether this is so or not, I observe a temporal difference in the development of the infraorbital canals between two species of *Barbus*. In specimens of *Barbus* cf. *paludinosus* of 17 mm SL the sensory canal of the 1st infraorbital (lachrymal) is present in the bone although it does not become completely enclosed until 24 mm SL. However, in *Barbus barbus* of 25 mm SL, the canal is subcutaneous and well-separated from the membranodermic part of the lachrymal. These species are respectively, tropical and temperate, and small and large sized. Thus, the variation in canal development may reflect the different temperature and hormonally controlled growth rates. In an adult specimen of *Barbus barbulus*, the posterior part of the canal lies subcutaneously, whereas the anterior part is attached to the lachrymal (Fig. 9c).

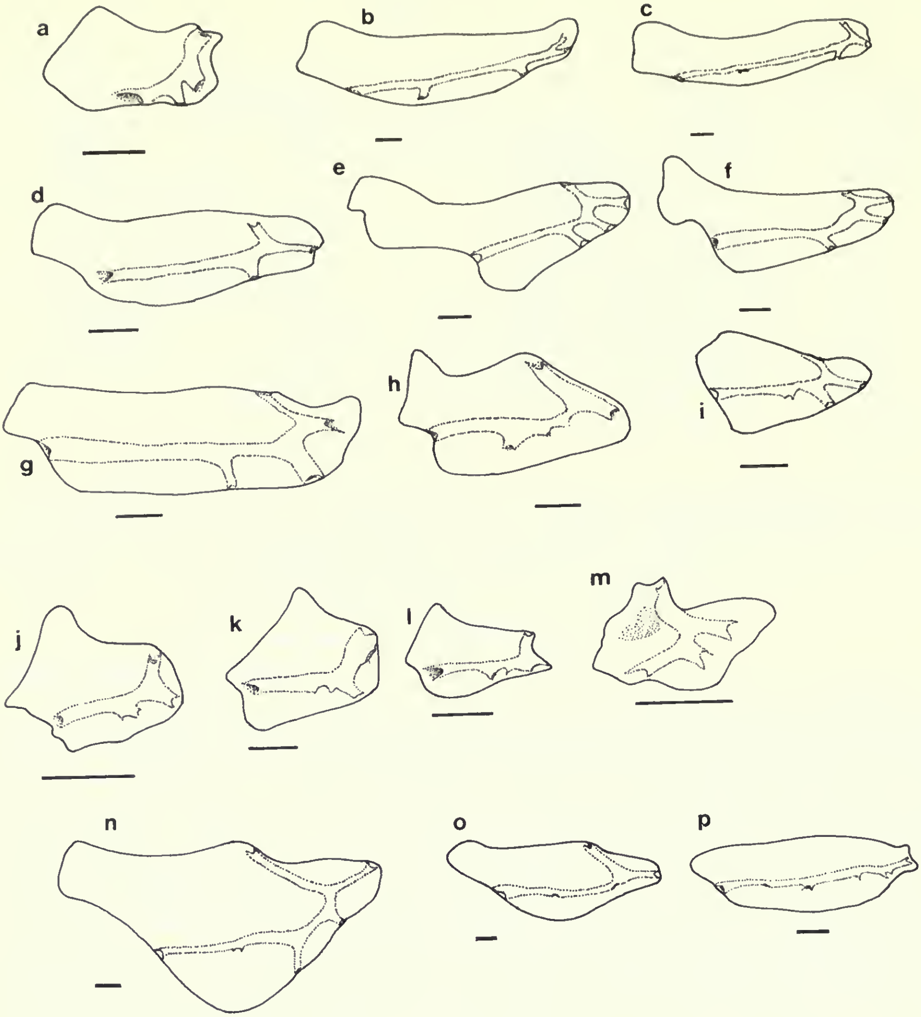

Fig. 10 Lachrymal (1st infraorbital) bones of; (a) *Barbus barbus* of 66 mm SL; (b) *B. barbus*, adult; (c) *B. comiza*; (d) *B. plebejus*; (e) *B. capito* (also in *B. sclateri*); (f) *B. bocagei* (also in *B. albanicus*); (g) *B. longiceps*; (h) *B. grypus* (also in *B. canis, B. sharpeyi, B. reinii*); (i) *B. intermedius intermedius*; (j) *B. trimaculatus*; (k) *B. altus*; (l) *B. callipterus*; (m) *Labeo coubie*; (n) *B. mursa*; (o) *B. serra*; (p) *B. andrewi*. Scale bars = 1 mm.

If Lekander (1949) is correct in recognising three distinct types of association between the laterosensory and membranodermic parts of the canal bones (at least amongst cypriniforms), then it may be that these represent arrest at successive ontogenetic stages. In this case, that exhibited by *Aulopyge* and some cobitids where the sensory and membranodermic components are separate represented the earliest, whilst that in which they are united, as in *Leuciscus*, would represent the most advanced ontogenetic stage.

The lachrymal in *Aulopyge* is virtually oblong in lateral view being somewhat tapered anteriorly. In most cyprinids the lachrymal is a deep, triangular or pentagonal bone, as in *Cyprinus, Labeo* and the majority of *Barbus* species (Figs 10i–m). In some Eurasian *Barbus* species, however, the lachrymal has the same oblong shape as in *Aulopyge*, and the sensory canal also runs in the ventral part of the bone. In this latter respect the Eurasian species also differ from other African and Asian *Barbus* where the canal runs centrally through the lachrymal (Fig. 10k). In *Barbus barbus*, one of the species with an oblong lachrymal in adults, there is a marked ontogenetic change in the bone's shape. In a specimen of 66 mm SL, it is almost square with a short, dorsally curved sensory canal (Fig. 10a). In adults, the bone is elongated, with a greatly lengthened canal (Fig. 10b), the anterior part of the canal having become more deeply forked and an additional pore developing at the posterior elongation of the canal.

The adult lachrymal morphology of *Barbus barbus* resembles that characteristic of certain other Eurasian species (Figs 9c, 10c, d, f & g). A variant of this condition is found in the Middle-eastern species *B. canis, B. sharpeyi, B. grypus, B. reinii* and the Asian *Barbus* (= *Tor*) *tor*, where the anterior part of the sensory canal runs close to the anterior border of the bone, and the dorsal border is concave (Fig. 10h).

It is difficult to evaluate the shape of the lachrymal as a phylogenetic character. Skelton (1980) pointed out that the South African West Cape species *Barbus andrewi* and *B. serra* possess a lachrymal of the same elongate form as that of the Eurasian species. However, the lachrymal of these two species differs from that in the Eurasian taxa in having the ventral border convex rather than straight (Figs 10o & p); see also p. 195.

My own comparisons permit the following generalisations:

*in all Leuciscinae the lachrymal has a square or even rounded, never elongate shape, even in those species with a relatively long ethmoid region (e.g. *Elopichthys bambusa*; Fig. 12A in Howes, 1978).

*in *Barbus* there is some degree of 'intermediacy' in shape between such forms as *B. trimaculatus* and *B. altus* (Figs 10j & k) and the *B. canis* type (Fig. 10h) exemplified by *B. oxyrhynchus* and *B. intermedius* (Fig. 10i).

*there is a distinct (?apomorphic) type characterising a group of Eurasian *Barbus* species; see above.

Vertebral column, dorsal and anal fins

The general morphology of the Weberian ossicles and centra of *Aulopyge* resembles that of *Barbus barbus*. In both taxa the neural complex is low, with a concave anterior border. Its posterior border is irregular and widely separated from the 4th neural spine, which is almost half the height of the neural complex and is inclined posteriorly.

Neural complex. The comparative morphology of the cyprinid neural complex has not been subject to any detailed treatment and from the following perfunctory observations appears worthy of closer study. The so-called 'neural complex' in cypriniforms is a supraneural having synchondral contact with the 3rd and 4th neural arches. There is usually a long gap between the supraoccipital and the neural complex and only rarely are they in close contact (see Reid, 1985). Within the Cyprinidae, two morphotypes of neural complex are recognisable (briefly described in Howes, 1981: 29–30; see also Chen *et al*, 1984); these can be correlated with the subfamily division already recognised as Cyprininae and Leuciscinae (see above and Appendix 2).

In Cyprininae, the neural complex is most often tall, axe-shaped and lamellate, with a vertical or forwardly inclined anterior border and without a grooved dorsal surface. The 4th neural spine is rarely as high as the neural complex, most often being half or less than half its height and narrowly separated from it. The first free supraneural never articulates directly with the neural complex.

In Leuciscinae, the neural complex is most often low, oblong or square, vertically or backwardly inclined; its dorsal surface contains a groove, and in some taxa, the neural complex is deeply forked (Howes, 1981, Fig. 22); the 1st free supraneural articulates with the groove (Howes, 1978: 19; Fig. 13). The 4th neural spine is most often as tall as the neural complex and may be widely separated from it.

The morphology of the neural complex is variable within the Cyprininae, but from the data at hand it is possible to make a broad and tentative classification. Within *Barbus*, the 'small' species examined (*B. radiatus, B. paludinosus, B. perince, B. leonensis, B. hulstaerti*) and some Asian taxa (including *B.* (= *Puntius*) *sophore*) possess a tall, oblong neural complex, either vertical or sloping backward and narrowly separated from the 4th neural spine which is the same height as the neural complex (Figs 11f–l).

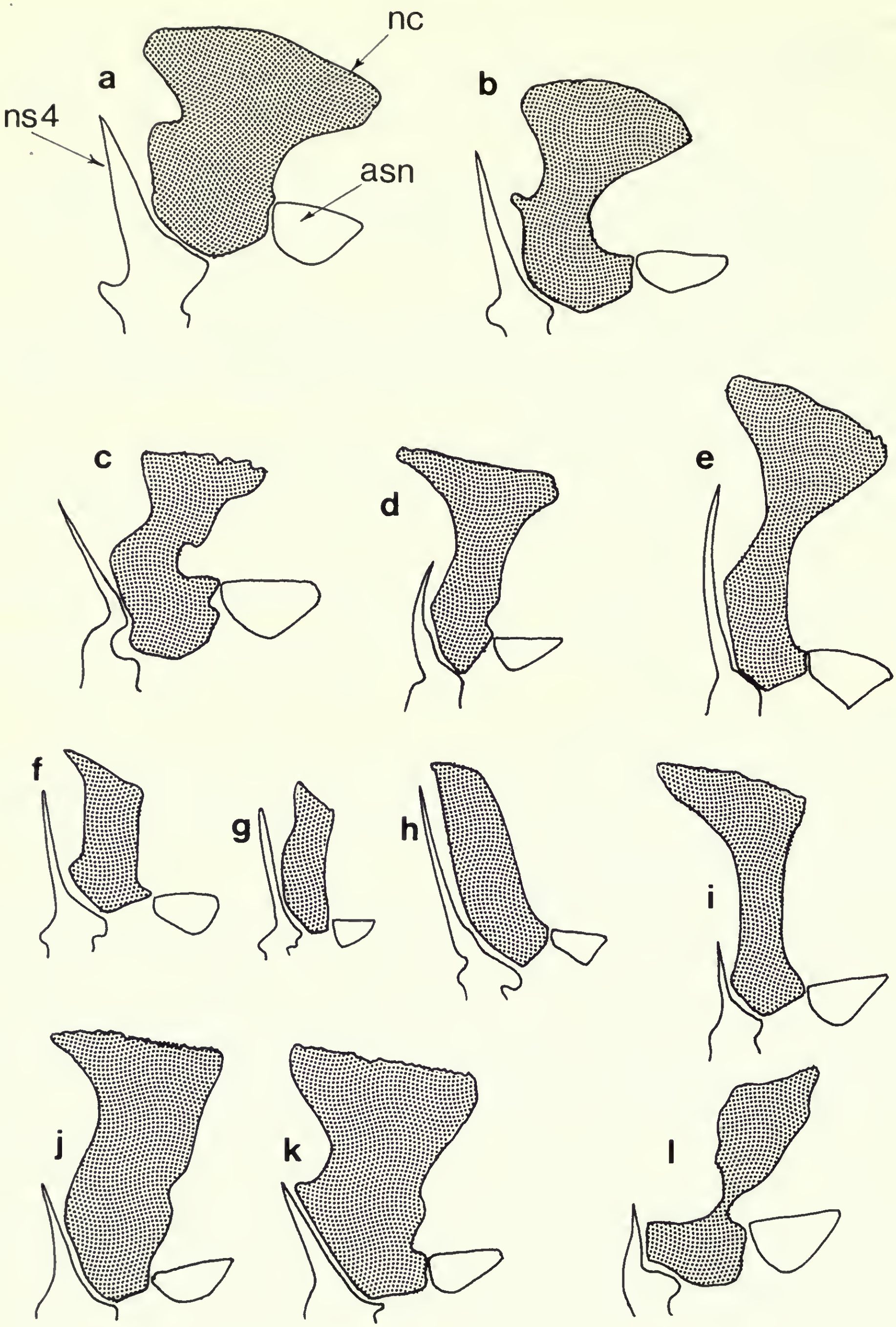

Fig. 11 Neural complex (shaded) and position of 4th neural spine in (a) *Aulopyge huegelii*; (b) *Barbus barbus*; (c) *B. plebejus*; (d) *B. altianalis radcliffi*; (e) *Cyprinus carpio*; (f) *Barbus paludinosus*; (g) *B. perince*; (h) *Puntius sophore*; (i) *Barbus marequensis* ('long-head morph'); (j) *Varicorhinus steindachneri*; (k) *V. ensifer*; (l) *Schizopygopsis stoliczkae*. Drawings made from radiographs, all to approximately the same scale.

Within the 'large' *Barbus* species, as in other Cyprininae, the neural complex is tall and axe-shaped. Its relationship to the 4th neural spine is variable. In some taxa the spine is short and curved forward, e.g. *B. intermedius, B. arabicus, B. altianalis* (Fig. 11d), *B.* (=*Tor*) *putitora, Carassius auratus*, or long and curved forward, e.g. *Cyprinus carpio* (Fig. 11e), *Cyclocheilichthys*, or short, vertical or sloping backward, e.g. majority of 'large' African *Barbus* (Fig. 11i), and some Asian *Barbus*. In some *Varicorhinus* species the spine is minute and barely developed as is also the case in *Cyprinion* species (see Howes, 1982). In all these taxa, however, the 4th neural spine is closely apposed to the posterior border of the neural complex (Fig. 11j).

As noted above, the neural complex of *Aulopyge huegelli* and *Barbus barbus* exhibit another morphotype (Figs 11a & b), being squat to oblong with a concave anterior border and an indented posterior border leaving a wide gap between it and the 4th neural spine. Other taxa with this morphology are the Eurasian, Middle-eastern and Chinese *Barbus* species *plebejus, nasus, meridionalis, barbulus, schejch, subquincunciatus* and *grahami*. An exaggerated variant of this condition occurs among the schizothoracin genera *Schizocypris* (Fig. 11l), *Diptychus, Gymnocypris* and *Schizothorax*, where the neural complex is irregularly shaped and widely separated from a small 4th neural spine.

From this limited survey it cannot be said which of these is a derived morphotype. That characteristic of *Aulopyge*, some Eurasian and Middle-eastern *Barbus* and schizothoracins may simply be a correlate of the generally elongate and depressed bodies of those taxa. There is also a degree of intraspecific and ontogenetic variability. For example, the ontogenetic sequence of neural complex development in the 'large' African *Barbus intermedius* is at 21·5 mm SL (Fig. 12a) that of the adult morphology (almost identical to that of *B. altianalis*, shown in Fig. 11d) in which the complex is narrowly separated from the 4th neural spine. At 25 mm SL the neural complex is tilted forward, is relatively taller and has a large gap separating it from the neural spine. At 31 mm SL the neural complex is upright and the 4th neural spine is tall and narrowly separated from it.

The four ontogenetic stages shown in Fig. 12 of specimens 21·5, 23·5, 25·0 and 31·0 mm SL seem to reflect four of the similar adult morphotypes described above.

To summarise the conditions of the neural complex among cyprinines:

*tall and oblong with long 4th neural spine—in 'small' African *Barbus* and (?all) Asian *Puntius*

*tall and axe-shaped with 4th neural spine closely apposed—in 'large' African and Asian *Barbus* and most other cyprinines, subgrouped as:

4th neural spine short—some African *Barbus* and other cyprinines
4th neural spine long—most African and Asian *Barbus*
4th neural spine minute—*Varicorhinus* and *Cyprinion*

*low, oblong or square with irregular anterior and posterior borders and with 4th neural spine widely separated posteriorly—in *Aulopyge*, Eurasian *Barbus* and schizothoracins

Vertebral number. Aulopyge has a total of 37–38 vertebrae, of which 10 (including the four Weberian vertebrae) are pre-dorsal, i.e. the neural spine of the last vertebra in the set lies in front of the 1st dorsal pterygiophore. This total vertebral number lies within the modal range for Cyprininae.

In a sample of 46 'large' African *Barbus* species the range is 36–42, of which 20 species have a range of 9–11 pre-dorsal vertebrae, 4 species have 11–12 (*oxyrhynchus, somereni, mariae* and *ethiopicus*) and the remaining 22 species have 13–17. These latter species, apart from the South African Cape *B. serra* and *B. andrewi*, are European and Middle-eastern species (Table 1). Schizothoracin genera have both higher total (46–48) and pre-dorsal (13–17) vertebral numbers (Table 2). In other Cyprininae, the numbers of pre-dorsal vertebrae rarely exceed 10; in *Cyprinion* there are 8–12, in *Cyprinus* 9–10, *Gibelion* 8 and *Catlacarpio* 8–9. In labeins, *Garra* has 9–12, and *Labeo* has 8–9. Squaliobarbin taxa also have a high pre-dorsal number, 10–12.

Skelton (1976) recorded the vertebral numbers in four groups of African *Barbus*, groupings made on the basis of scale striae pattern and degree of ossification in the last unbranched dorsal fin ray. He found higher counts in the group with parallel striated scales and with the dorsal fin ray ossified and smooth, a group to which belong the 'large' African *Barbus* species cited above.

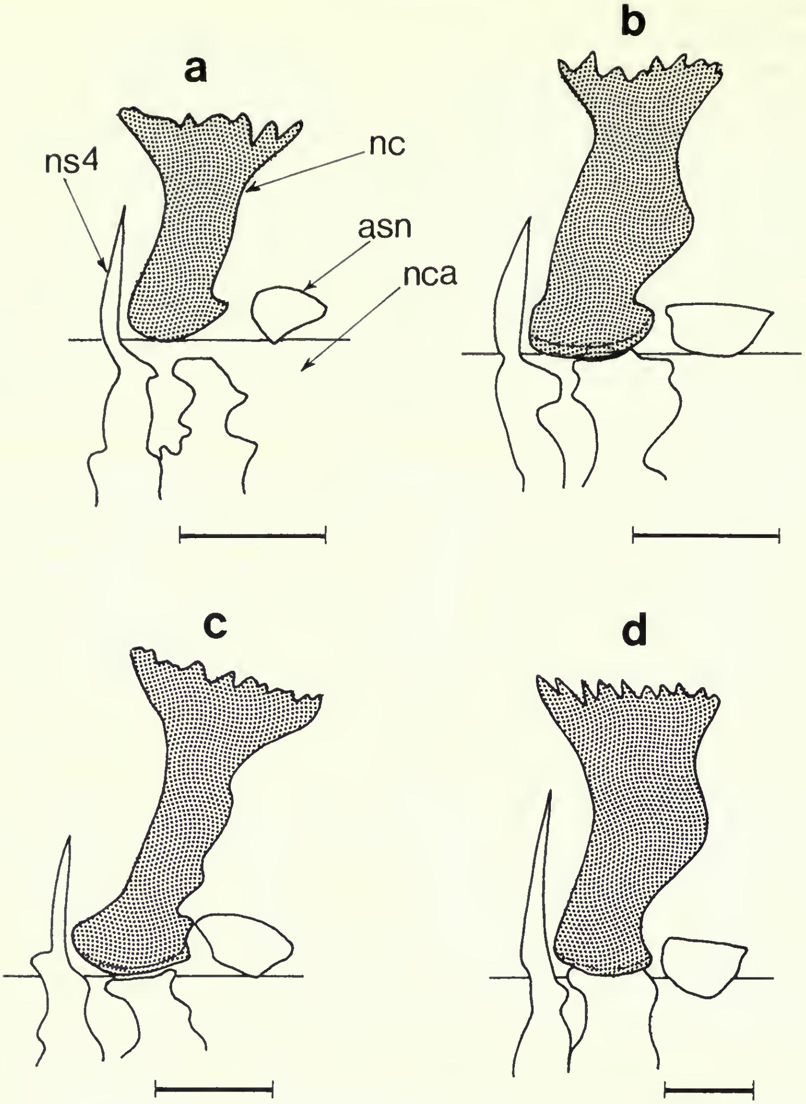

Fig. 12 *Barbus intermedius* Ontogenetic development of the neural complex, at (a) 21·5 mm SL; (b) 23·5 mm; (c) 25 mm; (d) 31 mm. Scale bars = 0·5 mm.

Following Lindsey's (1976) broader discussion of pleomerism, Skelton (1980) pointed out that Jordan's rule (the correlation of increased vertebral number with higher latitudes) may be a factor when considering, for example, the endemic high-latitude, high-altitude redfin '*Barbus*' which have a more frequently occurring range (36–38) than species of 'small' African *Barbus* (31–38). Skelton argues that such specialisation signifies that the higher vertebral number represents a synapomorphy, one he uses to recognise the redfin '*Barbus*' as a monophyletic group.

In the Cyprininae, the total vertebral number never exceeds 48, and the modal range is 38–40; in the Leuciscinae the total range is greater, being 33–61, as is the modal range of 40–45 (see Howes, 1978, Table 1). Perhaps more significant is the consistently higher range of pre-dorsal vertebrae in Leuciscinae, 10–19 *versus* 9–14 in Cyprininae. Howes (1978; 1984) considered a high number of vertebrae as a synapomorphy for the aspinin group of leuciscine cyprinids, since the range for this group exceeds that of other leuciscines in both abdominal and caudal vertebrae.

Table 1 Vertebral and lateral line counts in *Barbus* species having high total and pre-dorsal numbers of vertebrae and lateral line scales, and having a serrated last unbranched dorsal fin ray. In '*Barbus*' species with a pre-dorsal vertebral count of 9–11, the total count rarely exceeds 43.

Species	Total	Pre-dorsal	Lateral line scales
albanicus	44	14	57
andrewi	38–40	14–16	38–40
barbulus	44	13	52–54
barbus	46	14	55–63
bocagei	42–44	14–15	45–49
brachycephalus	47	11	63
capito	42–45	13	57–65
(including specimens labelled as *kersin*)			
comiza	43	12	48–50
(syntypes)			
esocinus	48	14	76–78
graellsi	42–43	14	47–52
grypus	44–47	13–14	40
lacerta	43	13	55–63
longiceps	43–44	13–14	51–60
meridionalis	40	13	48–60
mursa	43	14	90–97
nasus	43–44	13–14	49–78
plebejus	41–42	13–14	49–78
rajanorum	45–46	13–14	57–65
(including specimens labelled as *schejch*)			
sclateri	42	12	46–47
(syntypes)			
serra	39–41	14–17	42–43
sharpeyi	40–42	13–14	30–31
(lacks serrated last dorsal spine)			
subquincunciatus	45	13–14	80–84
xanthopterus	44	13	58–60

Table 2 Vertebral counts in a selection of schizothoracins.

Species	Total	Pre-dorsal
Diptychus dybowski	48	13
Diptychus maculatus	49	14
Gymnocypris sp.	46	14
Schizothorax dipogon	49	15
Schizothorax esocinus	46–47	16
Schizothorax chrysochlorus	42	14
Schizothorax grahami	47	16
Schizothorax intermedius	48	14
Schizothorax richardsoni	46	15
Schizothorax prenanti	46	15
Schizothorax sinuatus	48	16–17
Schizothorax yunnanensis	46	15
Schizopygopsis stoliczkae	48	15

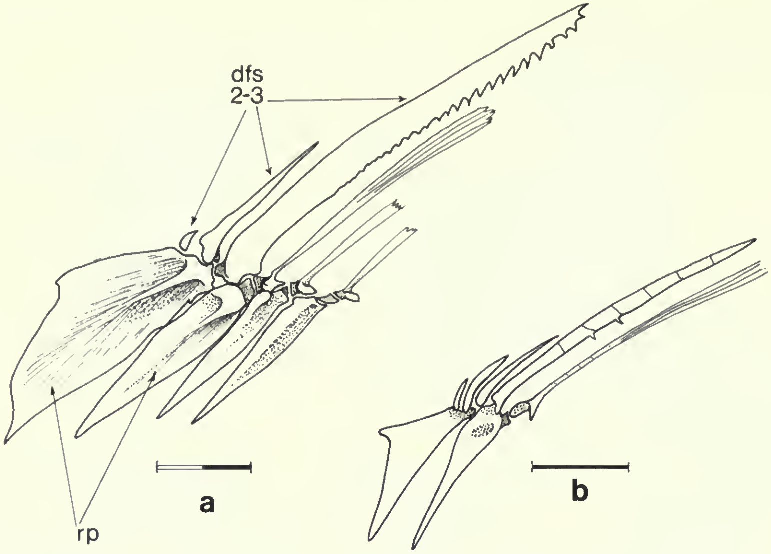

Fig. 13 Unbranched dorsal fin rays of, (a) *Aulopyge huegelii*, 115 mm SL; (b) *Barbus barbus*, 24 mm SL (cartilage stippled); scale = 1 mm.

It is difficult to assign polarity to vertebral number for other groups of cyprinids because,

*there is a continuum from the relatively low numbers in Cyprininae to the higher numbers in Leuciscinae

*there is the phenomenon of pleomerism (see Lindsey, 1975)

*vertebral numbers may be influenced by latitudinal position and temperature changes (see Lindsey, 1975; Lindsey & Arnason, 1981).

Lindsey (1975) commented that the Catostomidae display significant pleomerism among its species, but not in the family as a whole. The same observation can be applied to the Cyprinidae, where deep-bodied genera such as *Cyprinion* and *Megalobrama* have similar maximum lengths to those of cylindrical, depressed or compressed and slender forms, but possess lower vertebral numbers.

Dorsal fin and serrated unbranched dorsal fin ray. In Aulopyge the first (reduced) dorsal fin ray lies on a vertical just anterior to the base of the pelvic fin and above the 15th vertebra.

In those *Barbus* with a high number of pre-dorsal vertebrae the 1st dorsal fin ray lies above the 16th–18th vertebra and above or somewhat anterior to the origins of the respective fins. In the majority of the Cyprininae, the dorsal fin lies:

*above or anterior to the origin of the pelvic fins.

*rarely posterior to the pelvic fin origin, (e.g. '*Labeo*' *stoliczkae*, *Barbus paludinosus*, *B. serra*, some *Puntius* species).

In the Leuciscinae, however, only exceptionally does the dorsal fin originate in advance of the pelvics, (e.g. *Pogonichthys*). In both Cyprininae and Leuciscinae there are several taxa where the dorsal fin origin is immediately above the pelvic fin insertion. Such a situation occurs in both basal leuciscines with short, cylindrical bodies, (e.g. *Opsariichthys*, *Zacco*) and those with elongate, compressed bodies, (e.g. *Salmostoma*, *Macrochirichthys*). In cyprinines, this generalised position of the dorsal fin is present in many 'large' and 'small' African *Barbus* species. Skelton (1980) considered a dorsal fin posteriorly placed in relation to the pelvics as a synapomorphy uniting serrated-dorsal fin rayed redfin *Barbus* species. However, if one assumed the Cyprininae to be the derived sister-group of the Leuciscinae, such a posterior dorsal fin position may indicate the

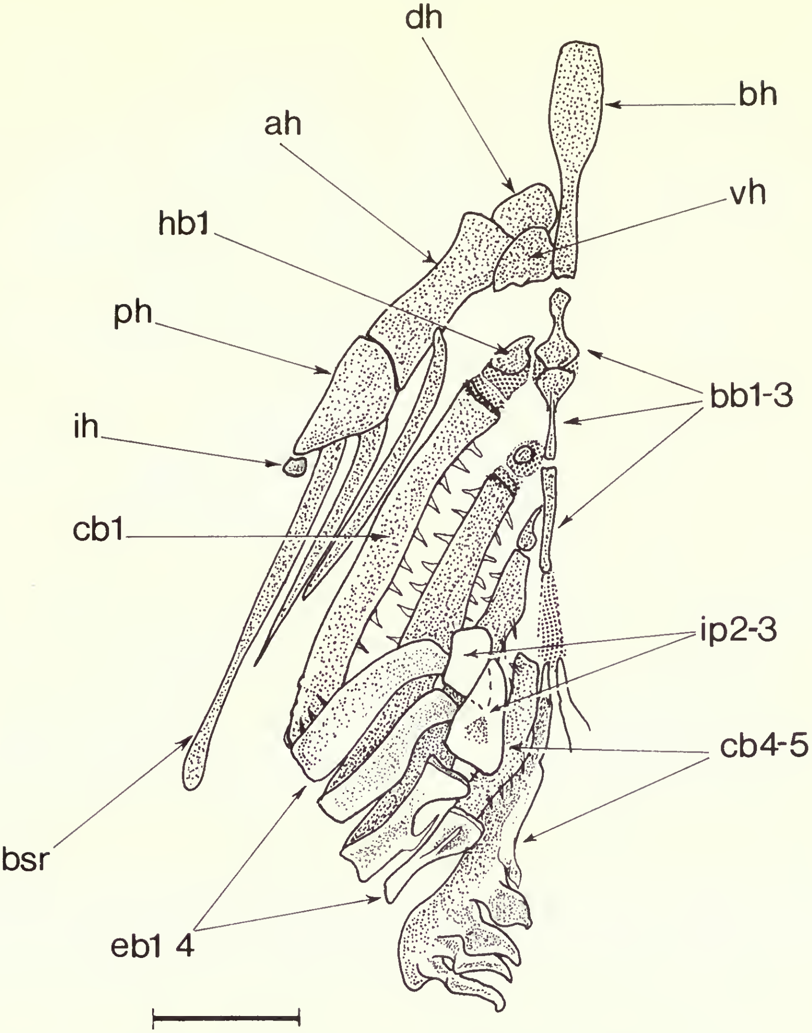

Fig. 14 *Aulopyge huegelii*, branchial arches of left side in dorsal view. Scale = 2 mm.

plesiomorphic condition. The forward placement of the dorsal fin in the Cyprininae, seen in its most extreme form amongst labeins, is more likely to be the derived state.

An analysis of the position of the 1st dorsal fin ray in relation to the vertebral column again reflects the major taxonomic grouping of the Cyprininae and Leuciscinae. In the majority of cyprinines, the 1st dorsal ray lies above the 11–18th vertebra (14–15th in *Aulopyge*), whereas in leuciscines, it may lie above any from the 16th to the 31st vertebra (modally between the 18th and 21st). The furthest posterior position of the 1st dorsal fin ray occurs in the chelin assemblage, where it lies above the 21st–26th vertebra in *Salmostoma* and the 30th–31st in *Macrochirichthys*. In the schizothoracins the 1st dorsal ray lies above the 17th–21st vertebra.

In *Aulopyge* there are 3 unbranched dorsal fin rays, the last being moderately serrated along its distal posterior border; there are 7–8 branched dorsal fin rays.

The number of unbranched dorsal fin rays preceding the 1st branched ray varies in the Cyprinidae from 2–6. Gosline (1978) found some significance in the numbers of unbranched dorsal

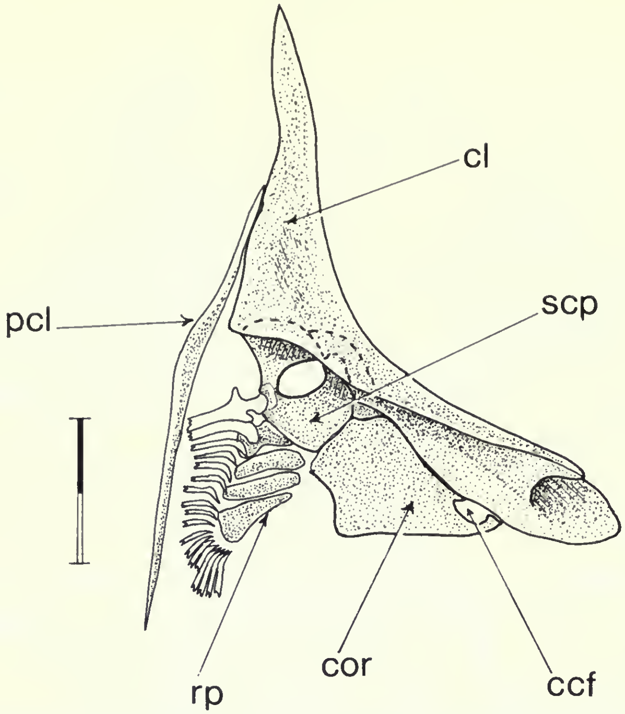

Fig. 15 *Aulopyge huegelii*, right pectoral girdle in lateral view. The (medial) positions of the mesocoracoid and part of the scapula are indicated by dashed lines.

fin rays, believing a modal count of 4 to be representative of the Cyprininae whilst 3 was present in '. . . other cyprinid subfamilies'. Although Gosline's subfamily concept differs from that presented here, I find his statement justified. A possible reason for there being a high number of unbranched dorsal fin rays in cyprinines may be correlated with the often marked ossification of the last such element. A large heavy spine-like ray, in order to remain rigid may require some anterior bracing in the form of several and strong elements in the fin.

Highly ossified dorsal rays rarely occur in the Leuciscinae, (e.g. *Capoetobrama*) and never bear serrations.

In the Cyprininae the last unbranched ray is always the largest but varies from flexible to heavily ossified, and may be smooth or serrated along its posterior margin. When present, a serrated ray may bear serrae over its entire or partial proximal length. A serrated dorsal ray occurs only in some species of the genera *Barbus*, '*Puntius*', *Schizothorax* and *Mystacoleucus*, while in other genera, such as *Acrossocheilus*, *Cyclocheilichthys* and *Cyprinus*, all species possess a serrated last unbranched dorsal ray.

Based principally on the classification of Boulenger (1911), Skelton (1976) recognised four group of *Barbus*, of which only one (Group III) contained species with a serrated dorsal fin ray. Within this group, the subgroup (IIIA) comprises the 'large' African *Barbus* and contains those species which also have relatively high total and pre-dorsal vertebral counts (see above, p. 179 and Table 1). The ranking of serrated dorsal fin rays as a synapomorphy is dubious since the feature has an irregular distribution among genera recognised as monophyletic, (e.g. *Cyprinion*; see Howes, 1982). However, it would be possible to test for the plesiomorphic nature of dorsal fin ray serrations by observing their presence in some ontogenetic stage of those taxa whose adults lack them. In *Barbus barbus*, in which the last unbranched dorsal ray bears serrations, they begin to appear at 23·5 mm SL when that ray is still segmented (Fig. 13b).

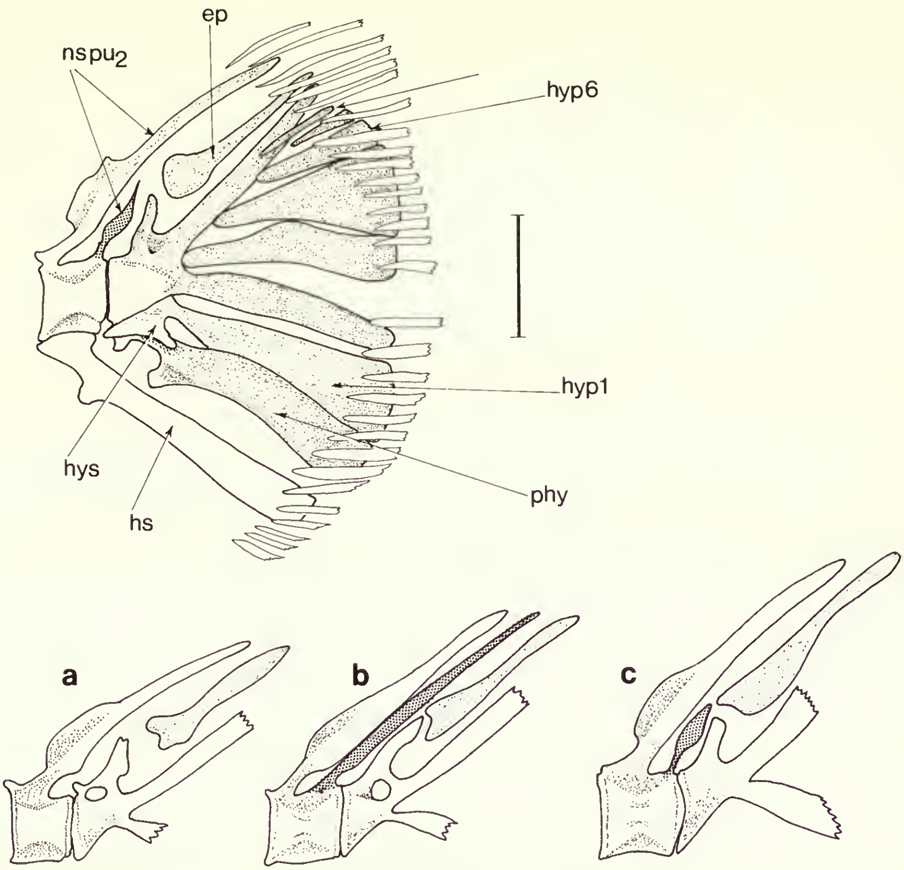

Fig. 16 *Aulpyge huegelii*, (above) caudal fin skeleton of 52 mm SL specimen. Scale = 1 mm; (below) variation on second neural spine (dark shading) on PU_2 of specimens (a) 106 mm, (b) 112 mm, (c) 127 mm SL.

Other osteological features

Aulopyge is conservative in its other skeletal elements.

The *gill arches* are of a generalised cyprinid type except for the complete absence of gill-rakers on the outer margin of the 1st ceratobranchial and only 3 or 4 rakers on the 1st epibranchial. The pharyngeal bone (5th ceratobranchial, Fig. 14) is broad and bears a single row of four teeth, the first somewhat globular with a prominent cusp, the others having bevelled or chisel-like crowns.

The *pectoral girdle* has a tall, upright cleithral limb and a short horizontal limb with a narrow lamina (Fig. 15). The cleithral-coracoid foramen is minute and the coracoid is small. The size of the cleithral-coracoid foramen is variable amongst cyprinids, both intra- and interspecifically (see Howes, 1979: 180), and appears to have little worth as a phyletic character. There is a single, long postcleithrum in *Aulopyge*.

The *caudal fin skeleton* is of a generalised type with 6 hypurals, a well-developed hypurapophysis, paired uroneurals and a long, proximally expanded epural (Fig. 16). There is, however, variable development in the neural arch on PU_2. In the smallest specimen available (52 mm SL) there are two neural arches on PU_2, the posterior arch having only a short spine (Fig. 16). In a specimen of 106 mm SL there are two arches with fully developed spines, and in the largest, 127 mm SL, the condition resembles that of the smallest specimen, namely, the second, posterior arch having a small neural spine (Figs 16a–c).

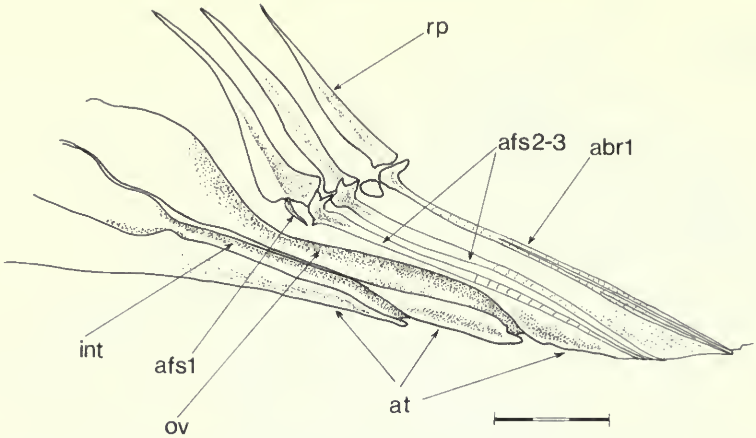

Fig. 17 *Aulopyge huegelii*, anal tube and anal fin of female. Drawn from dissection and X-Radiograph of 116 mm SL specimen.

Radiographs of a wide range of cyprinines reveal the presence of a second neural arch on PU_2 to be of not infrequent occurrence, although when it does occur, the neural spine is usually fully developed, (e.g. *Barbus plebejus, Barbus canis, Barbus micropogon, Barbus barbulus, Acrossocheilus yunnanensis, Carassius auratus*). A reduced second PU_2 neural spine is found in *Barbus comiza*.

The significance, phyletic or otherwise, of a second neural arch and spine on PU_2 is unknown. Its mosaic and wide distribution in cyprinines make polarity assignment impossible. It is of interest to note, however, that in leuciscines, it is the 3rd preural centrum which bears a double neural arch rather than the 2nd as in cyprinines (see Howes, 1984: 296). Variability of neural arches on the posterior caudal centra may be a plesiomorphic feature of teleosts; Greenwood (1970: 134) noted such variability in Elopiformes.

Sexual dimorphism and genitalia

Seeley (1886) pointed out the marked sexual dimorphism of *Aulopyge* exhibited in the morphology and position of the anal and genital openings and in the smaller body size of the male.

In the male *Aulopyge*, the anus and genital opening are separated, the genital orifice being posterior in position and lying in front of the first unbranched anal fin ray. In the female, both openings and their respective ducts are contained in a fleshy tube which is adnate to the 2nd unbranched anal fin ray. The oviduct is firmly joined to the flexible 2nd ray for part of its length (Fig. 17). In both males and females the 1st unbranched anal fin ray is vestigial and does not project from the body surface. The genital morphology of *Aulopyge* is unique among cypriniforms.

Discussion

Aulopyge relationships and barbin classification

Aulopyge exhibits a condition well known to cyprinid systematists, namely the possession of several unique features (autapomorphies) and few, if any, recognisable synapomorphies with other cyprinid taxa. Too few published comparative anatomical data exist for barbelled carps (Cyprininae) and the comparisons made during this study are of limited taxonomic scope. However, some information has emerged which may signpost useful characters for determining subgroups amongst barbins. The phylogenetic position of *Aulopyge* can only be discussed in the context of these wider issues.

It was stated in the Introduction that *Aulopyge* is a member of the Cyprininae. This subfamily was one of the divisions recognised by Howes (1981) on the basis of:

*a maxillary barbel associated with a foramen in the maxillary bone through which the barbel is supplied by a branch of the VII facial nerve.

*a rostrally extended supraethmoid with a laterally convex border.

At present only two monophyletic assemblages have been identified within the Cyprininae, *viz.* the *squaliobarbin group* (Howes, 1981) and the *labein group* (Reid, 1982; 1985). The former is a group of three seemingly plesiomorphic genera (*Ctenopharyngodon, Mylopharyngodon* and *Squaliobarbus*) having a native distribution restricted to China. The labeins are a speciose assemblage of *c.* 16 genera with an Afro-Asian distribution. *Aulopyge* shares none of those derived characters listed by Howes (1981) and Reid (1982; 1985) as defining either group.

The Cyprininae may be subdivided on the basis of the morphology of the dilatator fossa (Howes, 1981: 15). There are two conditions of the fossa; 1) it indents the dorso-lateral cranial surface, or 2) it is a foramen in the ventral lamella of the frontal, and in the case of the labeins, the sphenotic as well.

It is assumed from its widespread occurrence in teleosts, and its universal presence in all non-barbelled cyprinids (Leuciscinae) and other cyprinoids, that the dorsal cranial dilatator fossa represents the pleisiomorphic condition. That the ventral, foraminate dilatator fossa is a derived condition is reinforced by its ontogenetic history.

The development of the foraminate fossa was traced in a series of *Barbus intermedius* specimens 20–55 mm SL. In the smallest specimens the fossa is of the plesiomorphic type, (i.e. dorso-laterally placed and indenting the surfaces of the sphenotic and frontal); the *dilatator operculi* muscle is a narrow band-like element. At 29 mm SL there is a lateral process on both the frontal and sphenotic; the indentation for the muscle in the frontal has deepened. By 31 mm SL the sphenotic process has curved downward and the frontal lamella is perforated; the anterior part of the dilatator muscle runs through the foramen and fibres also originate from its lateral rim and the sphenotic process (Figs 18a–c). By 55 mm SL the foramen is well-formed and increased in size by medial attrition of the frontal lamella.

In the smallest specimens of *Barbus barbus* available (25 mm SL) there is no sign of a foraminate dilatator fossa and the condition resembles that in the smallest specimen of *Barbus intermedius*. It is reasonable to assume that the development of the fossa in this species proceeds along much the same course as that described in *B. intermedius*. In the two closely related species *Barbus litamba* from Lake Malawi and *B. mattozi* from the Limpopo, the fossa is foraminate only in specimens above 103 mm SL, and then only has a small opening.

Although it may be argued that a foraminate dilatator fossa could have been derived independently within different cyprinine lineages, it will be accepted as a working hypothesis that it is the principal synapomorphy for one group of Cyprininae. Since *Aulopyge* lacks a foraminate dilatator fossa it must be included with the squaliobarbins, schizothoracins, several *Barbus* species and other taxa listed in Table 3. Of these, the most likely candidate for sister-group relationship to *Aulopyge* is the schizothoracin assemblage. Some schizothoracin genera lack scales, possess a narrow ethmoid, serrated last unbranched dorsal fin ray and have a well-developed ventral facet on the lateral ethmoid, all derived characters shared with *Aulopyge*. However, these characters are mosaically distributed amongst schizothoracin species, no one taxon possessing all together, and so a relationship between *Aulopyge* would involve only certain species, thus making the schizothoracins a paraphyletic group. Previous authors, in recognising the subfamily Schizothoracinae *sensu* Berg, 1912, have tacitly assumed monophyly. Such an assumption is based on the possession by all included taxa of 'tile' scales, i.e. a row of regular, oblong scales at the base of the anal fin. This synapomorphy is supported by another, namely the presence of a bony strut extending from the parasphenoid to contact the prootics in the midline and thus dividing the posterior myodome. As such, this feature resembles the basisphenoid present in other teleosts, but which is absent in ostariophysans. These two characters indicate the monophyly of the schizothoracins and as such exclude *Aulopyge*, which lacks both of them.

Aulopyge also shares the character of well-developed lateral ethmoid and entopterygoid facets with *some* species of *Barbus*. This character distribution immediately raises the question; what is meant by *Barbus*?

At the present time *Barbus* includes *c.* 800 nominal species distributed in Eurasia and Africa,

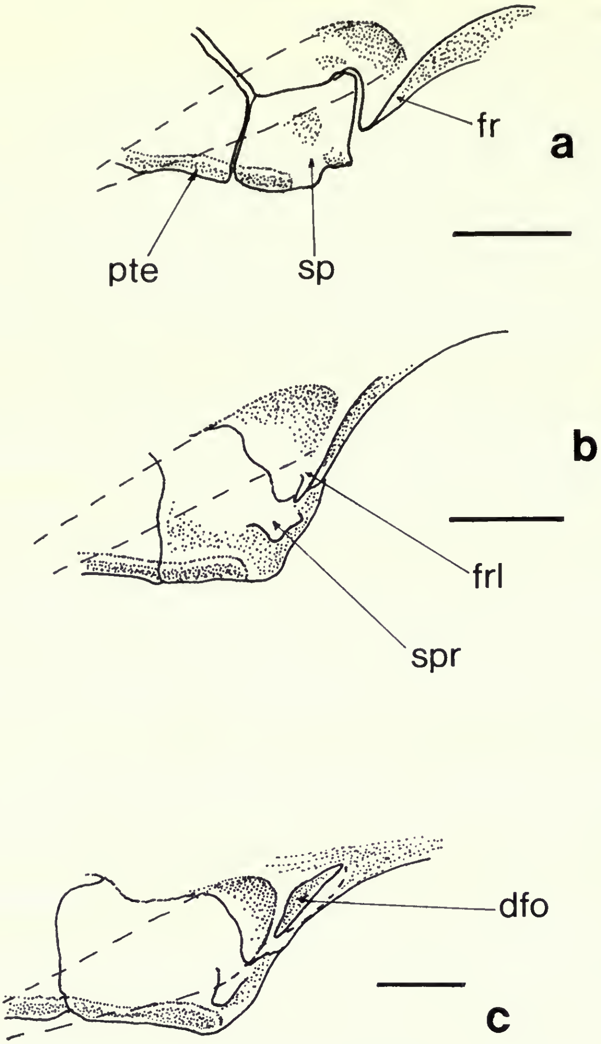

Fig. 18 *Barbus intermedius intermedius,* ontogenetic development of dilatator fossa; (a) at 21·5 mm; (b) at 25 mm; (c) at 31 mm SL. Dashed line indicates position of *dilatator operculi* muscle; all in ventro-lateral view. Scales = 0·5 mm.

many of which, even to the non-specialist, bear scant resemblance to the type species of the genus, the European *Barbus barbus* (Linn.). Some authors have opted to recognise separate genera, (e.g. *Puntius, Tor*) for Indian and South East Asian species, a solution which does little to elucidate relationships since these 'genera' are not defined on derived characters. The definition of *Barbus* can only be approached through an adequate anatomical comparison of the Eurasian and African species.

Comparisons and character analyses made during this study have demonstrated that a 'group' including the type species *Barbus barbus* and other Eurasian species can be defined on a suite of five characters:

1) shield-shaped supraethmoid (Fig. 19a)
2) oblong lachrymal with ventral sensory canal (Fig. 10b)
3) enlarged lateral ethmoid facet articulating with a well-developed entopterygoid facet (Fig. 5a)
4) 13–15 pre-dorsal vertebrae

Table 3 Distribution of the dilatator fossa morphotypes amongst examined Cyprininae.

Foramen present:

Single foramen

Acrossocheilus
Barbichthys
Barbus (part; see Table 4)
Capoeta
Carassius
Cyprinus
Probarbus
Varicorhinus

Double foramen

Catla
Cirrhina
Crossocheilus
Garra
Labeo
Labiobarbus
Lobocheilos
Osteocheilus
Semilabeo
Tylognathus (*sensu* Reid, 1985)
Typhlogarra

Foramen absent:

Ageniogarra
Aulopyge
Barbus (part; see Table 4)
Cyprinion
Mystacoleucus
Onychostoma
Prolabeo

and in the squaliobarbins
Squaliobarbus
Mylopharyngodon

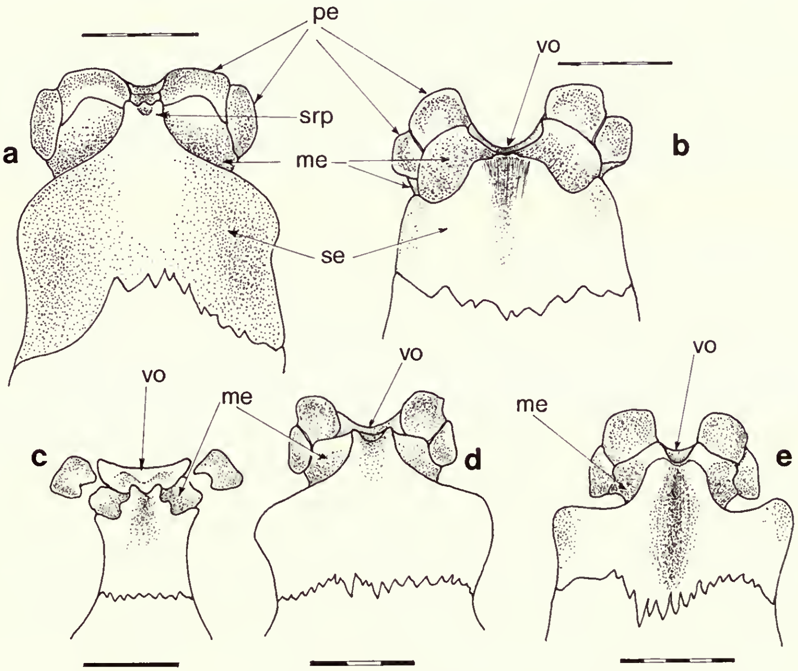

Fig. 19 Ethmoid region in dorsal view of, (a) *Barbus barbus*; (b) *B. altianalis altianalis*; (c) *B. leonensis* (scale bar = 0·5 mm); (d) *B. serra*; (e) *Tor putitora.*

Table 4 Condition of the dilatator fossa in 80 species of '*Barbus*'.

Foramen present

African species: *altianalis* (all subspecies), *andrewi, biscarensis, callensis, camptacanthus, fritschi, guirali, intermedius* (all subspecies), *jacksoni, johnstoni, litamba* (some, see text), *macrolepis, marequensis* (all morphs), *natalensis, nigrodorsalis, oxyrhynchus, progenys, reinii, rothschildi, serra, setivemensis, somerini, trimaculatus, tropidolepis.*
Eurasian species: *barbus, barbulus, bocagei, canis, comiza, douronensis, graellsii, grahami, hexagonolepis, longiceps, meridionalis, nasus, plebejus, sharpeyi, tambroides, tor, xanthopterus.*

Foramen absent

African species: *ablabes, amphigramma, argenteus, aspilus aurantiacus, dorsolineatus, eutaenia, holotaenia, hospes, hypsolepis, kersteni, leonensis, lineomaculatus, macrops, mimus, neglectus, neumayeri, paludinosus, paytoni, perince, poechi, profundus, radiatus, tenuis, thalamakanensis.*
Asian species: *aurilius, bimaculatus, binotatus, burmanicus, chola, collingwoodi, conchonius, filamentosus, pentazona, lithopides, orphoides, sarana, sophore, titteya.*

5) low neural complex widely separated from the 4th neural spine (Fig. 11b)

Of these only characters 1 and 2, because of their restricted distribution, can be treated as synapomorphies (character 2 is also shared with *Aulopyge*; see below). Characters 3–5, when viewed in the context of cyprinoid distribution are apparently derived. Their disparity among cyprinines, however, does not make them highly corroborated synapomorphies. Nonetheless they are congruent with characters 1 and 2.

If, on the basis of this character suite, *Barbus* is restricted to only some Eurasian species (see Appendix 1) then it remains to be determined how closely related it is to those African and Asian species presently included in *Barbus, Tor* and *Puntius*. From the distribution of the foraminate dilatator fossa (see above) it is clear that African and Asian barbins do not constitute a monophyletic assemblage. Of 80 African and Asian '*Barbus*' species selected at random, virtually 50% possess the character (41 with, 39 without; Table 4). Also emerging from this analysis is that almost none of the 'small' African *Barbus* examined possess a foraminate fossa. Thus, on the basis of the synapomorphic foraminate fossa, some *Barbus* species are more closely related to labein and other cyprinine genera such as *Capoeta, Cyprinus, Varicorhinus* and *Acrossocheilus* than to other *Barbus* species.

Immediate relationships of *Aulopyge*

Although it lacks a foraminate dilatator fossa, *Aulopyge* shares with some Eurasian *Barbus* species (termed from hereon *Barbus sensu stricto*) well-developed lateral ethmoid and entopterygoid articular facets and an oblong lachrymal with a ventral sensory canal (although in *Aulopyge* the canal is not fused with the bone; see p. 174. The lack of a foraminate fossa may be interpreted either as a loss or as a plesiomorphic condition, in which case the lateral ethmoid-entopterygoid facets and oblong lachrymal must be viewed as having been independently derived. Fewer assumptions are required to support the 'loss' of the derived dilator fossa in *Aulopyge* than are demanded by other schemes of relationship (Figs 20A–C). Support for 'loss' is that *Aulopyge* exhibits heterochrony in the late development and fusion of infraorbital sensory canals and in the absence of scales. It may be that the dorso-lateral dilatator fossa is also the retention of an early ontogenetic stage (see p. 187). Outright dismissal of independent origin on grounds of parsimony must be treated with caution, however, since it is noted that amongst the schizothoracins a lateral ethmoid facet is present in some taxa (p. 170). Since the schizothoracins are almost certainly a monophyletic group within the Cyprininae (see p. 187) it follows that this feature has been derived independently from that in *Aulopyge, Barbus, sensu stricto* and other barbins (including *Cyprinus*).

Whether *Aulopyge* is recognised as the sister-group to *Barbus sensu stricto*, or to *Barbus sensu*

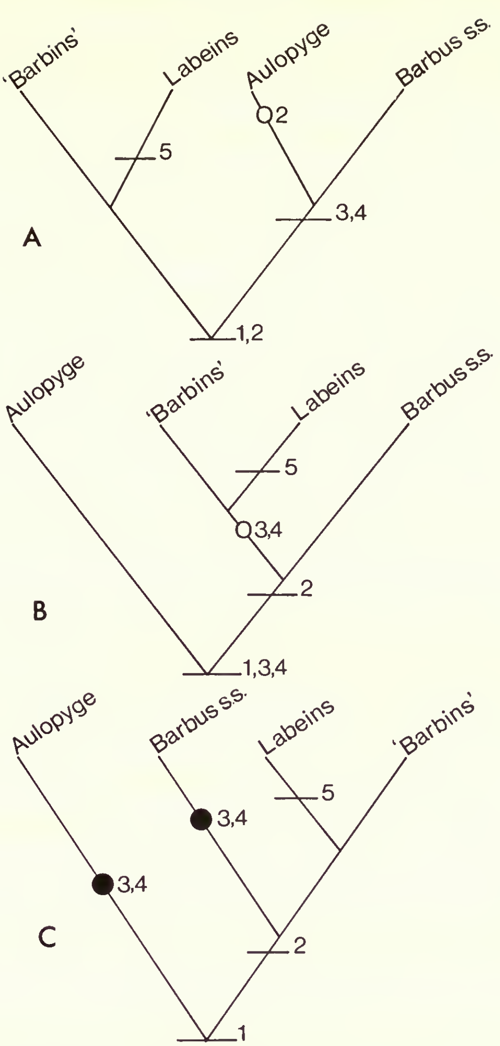

Fig. 20 Three possible schemes of relationship between *Aulopyge* and other cyprinines. A, the most parsimonious, involves the loss of character 2 in *Aulopyge*. B. involves the loss of characters 3 and 4 in 'Barbins' and Labeins. C, involves independent derivation of characters 3 and 4 in *Aulopyge* and *Barbus sensu stricto*.

Character 1. lateral ethmoid articular facet; 2. foraminate dilatator fossa; 3. expansion of lateral ethmoid facet and presence of entopterygoid facet; 4. oblong lachrymal; 5. double-foraminate fossa (additional characters defining Labeins are given in Reid, 1985). 'Barbins' include those taxa listed in Table 3, under 'foramen present'.

stricto plus other barbins and labeins cannot be resolved on those characters considered here. However, no synapomorphies have been identified that would suggest *Aulopyge* is more closely related to any cyprinine taxon lacking a foraminate dilatator fossa, including the schizothoracins.

Karaman's (1971) hypothesis of an intermediate taxonomic position for *Aulopyge* between 'barbine' and 'schizothoracine' subgroups (see above, p. 165) is not supported by this study. Schizothoracins do share with *Barbus sensu stricto* high total and pre-dorsal numbers of vertebrae (Table 2), but the polarity of this character is uncertain (see p. 182) and if treated as a synapomorphy in a scheme of relationship involving *Aulopyge, Barbus* and 'other cyprinines' it is incongruent with other synapomorphies.

I have found no evidence in support of Arai's (1982) contention that *Aulopyge* possesses some gobionine characters.

From the data analysed two hypotheses are available:

**Aulopye* is a derived member of the *Barbus sensu stricto* lineage, with specialisation through reduction and 'loss' (Fig. 20A)

**Aulopyge* is a member of the 'stem-group' of Eurasian plus African barbins (Figs 20B & C).

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Appendix 1
The genus *Barbus sensu stricto*

Definition and included species

Banister (1980) placed the majority of Middle-eastern *Barbus* into two groups—the 'European' and 'Afro-Indian', which he characterised on overall morphology, scale type and serrated or smooth last dorsal fin ray. Banister stated that both groups might be monopyletic and so tacitly restricted *Barbus* to the 'European' group.

Lévêque & Daget (1984) stated that 'Strictly speaking the generic name *Barbus* shall be restricted to European and some north-African species'. These authors' remarks are supported by this study and reference has been made in the text to *Barbus sensu stricto*. Only a thorough comparative anatomical study of 'barbins' will provide a strict diagnosis (based on synapomorphies) of *Barbus*. The definition of *Barbus* used here is based on the characters analysed above and forms a working hypothesis for a more critical evaluation. Those taxa not embraced by this definition are referred to as '*Barbus*' or *Barbus sensu lato*; in the case of the Asian species, the generic names *Puntius* and *Tor* are already widely used (see for example, Jayaram, 1981). For African '*Barbus*' several generic names are available (see synonymy in Lévêque & Daget, 1984).

Barbus sensu stricto is defined on the basis of its members having a total vertebral count of 40–48 of which 13–15 are pre-dorsal vertebrae; a well-developed, centrally to anteriorly situated ventral lateral ethmoid facet articulating with a well-developed anterodorsal entopterygoid facet; a 'shield'-shaped supraethmoid with (usually) a prominent rostral process (Fig. 19a); neural complex low with a deeply indented anterior border, its posterior border (usually) well-separated from the 4th neural spine which is at least half the height of the neural complex; lachrymal elongate, often oblong with tapered anterior tip and sometimes an indented posteroventral border, sensory canal running through the lower half of the bone; 49–90 scales in the lateral line, (cf. 20–55 in African and Asian '*Barbus*').

Almaça (1981) distinguished three groups of Eurasian *Barbus* on the basis of lateral line scale counts but he pointed out the lability of this character due to influences of temperature and latitudinal variation (see similar remarks under 'vertebrae', p. 182).

The following species are considered to constitute *Barbus sensu stricto*:

Barbus albanicus Steindachner, 1870 (including *B. graecus* (Steindachner, 1895))
Distribution: Albania–Greece
Barbus barbus (Linnaeus, 1758), type species of the genus.
Distribution: Europe (see Almaça, 1981 for detailed distributional data and recognition of subspecies)
Barbus barbulus Heckel, 1846
Distribution: Tigris
Barbus bocagei Steindachner, 1865
Distribution: Iberia
Barbus capito (Güldenstädt, 1773)
Distribution: Caspian and Aral Sea basins; Amu Darya
Barbus comiza Steindachner, 1865
Distribution: Iberia

This species is included in *Barbus* on the basis of its possessing a high vertebral number, and a typical oblong lachrymal (Fig. 10c). However, it differs from other species in its longer and narrower head (see Almaça, 1967; 1972), concave dorsal profile, lower number of pre-dorsal vertebrae (12, cf. 13-15), tall neural complex narrowly separated from the 4th neural spine, and the absence of a fleshy overhanging upper lip. In its striking dorsal and lateral head profiles, and narrow ethmoid *B. comiza* greatly resembles *Aulopyge*. However, no synapomorphies have been identified that would suggest these features are anything other than homoplasies.

Barbus esocinus (Heckel, 1843)
Distribution: Tigris-Euphrates
Barbus graellsi (Steindachner, 1866)
Distribution: Portugal
Barbus lacerta Heckel, 1843
Distribution: Tigris-Euphrates and Qwarq rivers
Barbus longiceps Valenciennes, 1842
Distribution: Jordan River system
Barbus lorteti Sauvage, 1882
Distribution: Orontes R.
Barbus microcephalus Almaça, 1967
Distribution: Iberia
Barbus meridionalis Risso, 1826 (including *B. peloponnesius* Val., 1842).
Distribution: NE Spain—S. France—Yugoslavia—Greece
Barbus nasus Günther, 1874
Distribution: Morocco
Barbus pectoralis Heckel, 1843

Distribution: Orontes R.
Barbus plebejus Bonaparte, 1839 (including the subspecies recognised by Almaça, 1981; 1983)
Distribution: N. Italy–Greece
Barbus rajanorum Heckel, 1843
Distribution: Tigris-Euphrates

Karaman (1971) considers *B. schejch* (Heckel, 1843) and *B. barbulus* Heckel (listed here as a separate species), to be synonyms of *B. rajanorum*. This synonymy is doubtful and the '*rajanorum* complex' requires a taxonomic reappraisal. In Dr F. Krupp's opinion (pers. com.) *B. rajanorum* is a hybrid between *B. pectoralis* and *Capoeta damascinus*.

Barbus sclateri Günther, 1868
Distribution: Iberia
Barbus subquincunciatus Günther, 1868
Distribution: Tigris-Euphrates
Barbus steindachneri Almaça, 1967
Distribution: Iberia
Barbus xanthopterus Heckel, 1843
Distribution: Tigris-Euphrates

Although the Middle-eastern species *Barbus grypus* and *B. sharpyei* have relatively high vertebral numbers (Table 1), they lack the elongate lachrymal of the other species listed and possess, in common with *B. canis* and *B. reinii* what is considered to be another derived form of lachrymal in which the sensory canal runs along the anterodorsal border (see p. 177). *Barbus canis* and *B. reinii* both have low vertebral numbers, respectively 38—39 and 37 (totals) and 10 and 10–11 predorsal elements. *Barbus sharpyei* differs from other species of this group in having only 30–31 lateral line scales.

The systematic positions of *Barbus brachycephalus* Kessler, 1872 and *B. mursa* (Güldenstädt, 1773)

The generic placements of these two south Central Asian species (respectively the Aral and Caspian Seas and the Kura system) are problematical. Both species although having high vertebral counts differ in several ways from *Barbus sensu stricto* and other species of '*Barbus*'.

Barbus brachycephalus has rather slender barbels, unlike the thick, often papillate barbels of 'typical' species of the genus, and 7 branched dorsal fin rays, cf. 8 in the majority of *Barbus sensu stricto* and also in *Barbus sensu lato*. The cranium is broad and flat, lacking the transverse convexity of most barbins. There are a total of 47 vertebrae, but only 11 are predorsal, cf. 13–15 in *Barbus sensu stricto*.

Barbus mursa has a deep lachrymal with an anterior branching pattern resembling that of *Barbus canis* and related species discussed above (Fig. 10n). However, it possesses a series of preanal scales and a prominent genital papilla more reminiscent of schizothoracins.

The systematic positions of *Barbus andrewi* Barnard, 1937 and *B. serra* Peters, 1864

These two species are restricted to the South African Western Cape. On the basis of the characters given for *Barbus sensu stricto* both species should be included. Both, however, have a higher predorsal vertebral count than other *Barbus sensu stricto,* viz.: 14–17, cf. 13–15, but, a relatively low total vertebral number, viz.: 38–41, cf. 40–47. The supraethmoid has the same 'shield'-shaped appearance as in *Barbus sensu stricto* (Fig. 19d), but the vomer is broader anteriorly and extends further dorsally in *B. serra* and *B. andrewi*. Again, the lachrymal bones of the two species, while having the same overall appearance of that bone in the Eurasian *Barbus* have a sloped, rather than a perpendicular posterior margin and more convex ventral border. Because of these differences I am hesitant to include the Cape species in *Barbus sensu stricto*. According to Skelton (1980), *Barbus serra* and *B. andrewi* are sister-taxa, not closely related to any African '*Barbus*' he examined.

Appendix 2

Characteristics of the subfamilies Cyprininae and Leuciscinae

	Cyprininae (including 'Schizothoracinae')	Leuciscinae
1	Maxillary barbel present	No maxillary barbel
2	Maxillary foramen	No maxillary foramen
3	Supraethmoid with medially indented rostral process	No supraethmoid rostral process
4	Articular facets present on lateral ethmoid and entopterygoid in some taxa	Articular facets absent (except in *Tinca*)
5	Single, strong ligament connecting posterior face of lateral ethmoid with dorsomedial surface of entopterygoid	Connection between lateral ethmoid *via* connective tissue sheet, sometimes thickened laterally
6	Lachrymal (1st infraorbital) sometimes elongate and oblong	Lachrymal never elongate or oblong
7	*Dilatator operculi* muscle sometimes originating from ventral surface of the frontal and passing through a frontal-sphenotic foramen	*Dilatator operculi* muscle confined to cranial surface; fossa never foraminate
8	Neural complex lacking grooved dorsal surface; sometimes close to, or even contacting the cranium (supraoccipital)	Neural complex with grooved dorsal surface, never contacting the cranium
9	1st free supraneural not contacting neural complex	1st free supraneural articulating with neural complex
10	Dorsal fin origin lies above or anterior to that of the pelvics (rarely posterior)	Dorsal fin origin rarely above or in advance of the pelvics
11	1st unbranched dorsal fin ray lies above the 11th–18th vertebra	1st unbranched dorsal fin ray lies above 16th–31st vertebra
12	Last unbranched dorsal fin ray often serrated	Last unbranched dorsal fin ray never serrated
13	Modal number of vertebrae 38–40 (never exceeding 48)	Modal number of vertebrae 40–45 (range 33–61)

Note: The genus *Tinca* is included here in the Leuciscinae, although possessing a cyprinine feature (character 4). Chen *et al.* (1984) consider *Tinca* to be the sister-group of the Cyprininae (their 'Barbines'). Although for the most part, these authors appear to base their hypothesis on differences rather than on shared homologies, their cladogram requires serious consideration and offers a much needed, testable classification of the Cyprinidae.

British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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Zoology series Vol 52 No 6 25 June 1987

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Revision of the genera *Acineria*, *Trimyema* and *Trochiliopsis* (Protozoa, Ciliophora)

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Synopsis

The genera *Acineria, Trimyema* and *Trochiliopsis* are reviewed. The revision is based on an investigation of each of the type-species, namely *Acineria incurvata* Dujardin, *Trimyema compressa* Lackey, and *Trochiliopsis opaca* Penard, which were found in a sewage-treatment plant. *Acineria* comprises three species; *A. incurvata, A. nasuta,* and *A. uncinata. A. acuta* is a synonym of *A. incurvata. Trimyema* comprises eight species; *T. alfredkahli, T. claviformis, T. compressa, T. echinometrae, T. kahli, T. marina, T. minuta* and *T. pleurispiralis* but *T. alfredkahli* and *T. claviformis* are perhaps synonyms of *T. marina. Trochiliopsis* is monotypic and new for the fauna of Austria. This genus is apparently closely related to the autochthonous soil ciliate *Stammeridium kahli.*

Zusammenfassung

Die Gattungen *Acineria, Trimyema* und *Trochiliopsis* werden revidiert. Die Revision basiert auf der Untersuchung der Typusarten, nämlich *Acineria incurvata* Dujardin, *Trimyema compressa* Lackey und *Trochiliopsis opaca* Penard, die in einer Kläranlage gefunden wurden. Die Gattung *Acineria* umfasst drei Arten; *A. incurvata, A. nasuta* und *A. uncinata. A. acuta* ist ein Synonym von *A. incurvata.* Von *Trimyema* sind acht Arten beschrieben; *T. alfredkahli, T. claviformis, T. compressa, T. echinometrae, T. kahli, T. marina, T. minuta* und *T. pleurispiralis. T. alfredkahli* und *T. claviformis* sind möglicherweise Synonyme von *T. marina. Trochiliopsis* ist monotypisch und neu für die Fauna Österreichs. Diese Gattung ist höchstwahrscheinlich nahe verwandt zum autochthonen Boden-Ciliaten *Stammeridium kahli.*

Introduction

Only few activated-sludge ciliates have been characterized by silver-staining techniques which is sometimes necessary for their correct identification. To overcome this deficiency, a project to redescribe the most frequently occurring species was begun. During these studies the poorly known type-species of the genera *Acineria, Trimyema,* and *Trochiliopsis* were found. They have been reinvestigated using modern techniques which provide a base upon which to revise these genera.

Supported by the 'Fonds zur Förderung der wissenschaftlichen Forschung, Projekt Nr. P 5889'.

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Materials and Methods

Acineria incurvata, Trimyema compressa, and *Trochiliopsis opaca* were obtained from activated sludge of the sewage-treatment plant at Aspach, Upper Austria.

Small samples of activated sludge were placed in glass petri-dishes where they remained without additional aeration. In such cultures a surprising succession and enrichment of ciliates often occurred. *Acineria incurvata* could also be cultured in tap water enriched with a crushed wheat grain which supported the growth of many small prey ciliates (*Dexiotricha, Uronema*).

The infraciliature was revealed with a protargol silver-staining method (Foissner, 1982). The silverline system was studied in specimens impregnated by a modified 'dry' silver-impregnation technique (Foissner, 1976). The oral structures of *Trimyema compressa* were impregnated by the pyridinated silver carbonate method of Fernandez-Galiano (1976) as improved by Augustin *et al.* (1984).

For scanning electron microscopy *Acineria* cells were fixed for 10 minutes in Parducz's solution (2% OsO_4 and concentrated Hg-sublimate solution, 4 : 1), rinsed in 0·05 M sodium cacodylate buffered at pH 6·3, dehydrated in an isopropyl alcohol series (60%, 70%, 80%, 90%, 100%, 100%, five minutes each) and put into a mixture of isopropyl alcohol (100%) and frigen 11 (2 : 1, 1 : 1, 1 : 2, five minutes each). Finally, cells were transferred into pure frigen 11 and critical point dried, using frigen 13. Specimens were gold-sputtered three times for six minutes each.

Each species was drawn from life as well as from impregnated specimens using a camera lucida for the latter. The drawings are only slightly diagrammatic. All statistical procedures follow methods described in Sokal & Rohlf (1981).

Genus *ACINERIA* Dujardin, 1841

DIAGNOSIS. Amphileptidae Bütschli, 1889 with (1) compressed oral slit anteriorly rolled up and overlapping to the left side forming (together with the anterior dorsal margin) an oblique spoon-like excavation, (2) three perioral kineties (one left and two right of the cytostome, (3) somatic kineties on the right side successively shortened along the cytostome, (4) oral slit measuring less than half of body length being located at the convex side of the tapering anterior. Freshwater and marine, prefers polysaprobic conditions.

TYPE-SPECIES. *Acineria incurvata* Dujardin, 1841

REMARKS. *Acineria* was mentioned for the first time by Dujardin (1840) in the family 'Trichodiens' but without any valid characterization. In 1841 he gave a rather vague diagnosis of the genus and of two species. Maupas (1883) criticized the unsatisfactory diagnosis and gave a better description of *Acineria incurvata* even noting the overlapping anterior end which is the main character of *Acineria*; nevertheless, he did not include this character in the diagnosis. How Maupas (1883) arrived at the conclusion that his species was the same as that described by Dujardin remains, however, inexplicable. It was only Kahl (1926) who used the real character of the overlapping dorsal end of the mouth to the left side to distinguish *Acineria* from the most closely related genus *Litonotus*. But there is no indication in the infraciliature that the dorsal margin and the left side coalesce as supposed by Kahl (1926, 1931). Thus, Kahl's interpretation that a part of the ciliated right side of the genus *Litonotus* has shifted over to the left side in *Acineria* is not supported by our investigations. We consider the rolled up anterior part of the mouth to be the reason for the anterior overlapping of the dorsal margin. The occurrence of somatic kineties on the left side, as stressed by Kahl (1926) is a weak distinctive character because this happens also, more or less pronounced, in the genera *Litonotus* and *Amphileptus* (Foissner, 1984).

Key to the species

1a Single spherical macronucleus . . . . ***A. nasuta***
1b Macronucleus in two parts with a single micronucleus between them 2
2a Cytostome restricted to the rolled up anterior pole, right side with 3 somatic kinetics, left side unciliated . . . . ***A. uncinata***
2b Cytostome about one third of body length, 10–12 normally ciliated somatic kineties ***A. incurvata***

Descriptions of species

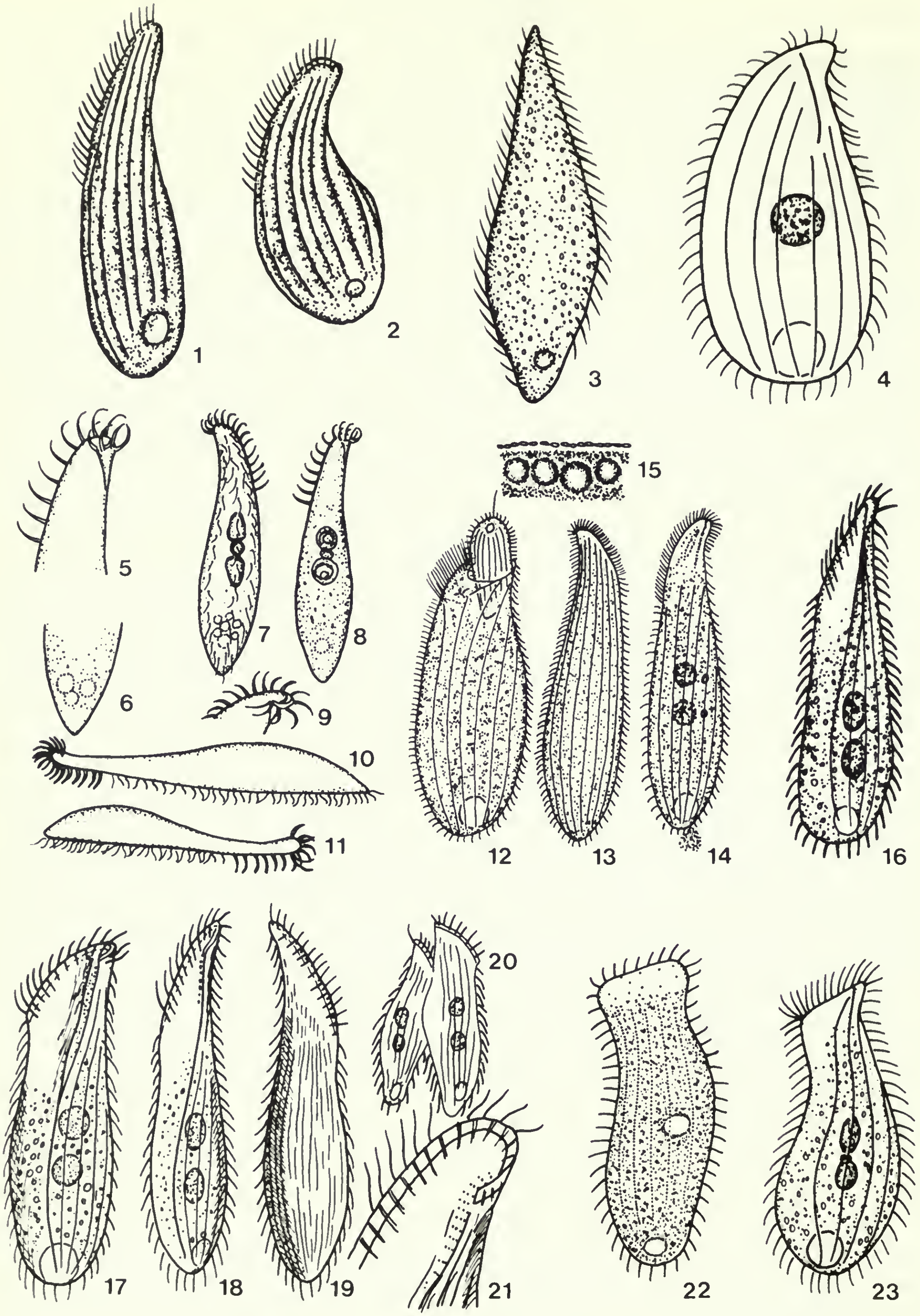
Acineria incurvata Dujardin, 1841

?Trachelius anaticula Ehrenberg, 1833
Acineria acuta Dujardin, 1841
?Amphileptus anaticula Claparède & Lachmann, 1859
Lionotus reversus Kahl, 1926
Amphileptus incurvatus Lepsi, 1926*a*
Litonotus lamella Fryd-Versavel *et al.*, 1975

NEOTYPE-SPECIMENS. Slide (protargol silver impregnated) of neotype-specimens has been deposited in the British Museum (Natural History) in London, reference number 1986:5:30:1.

REDESCRIPTION (Figs 1–3, 12–58, Table 1). Type species of the genus. Freshwater and marine. About 45–200 µm (Dujardin, 1841; Maupas, 1883; Kahl, 1926, 1928, 1931, 1933; Horváth & Kuhn, 1941; Bick, 1972; Foissner, 1977/78). Abnormal, giant individuals up to 500 µm showing most organelles duplicated observed by Foissner (1977/78) and probably by Lepsi (1965) (Figs 28–30). Body oblong, slightly contractile, laterally compressed, rounded posteriorly, narrowing anteriorly to a blunt point. Rather variable in shape (slender to wide and plump) depending on nutritional condition (Figs 31–34). Ventral side more or less convex, dorsal side straight or concave in the anterior, convex in the posterior region. Excavated region conspicuous, shining brightly. Anterior-most dorsal top somewhat refractive, due to the rolled up oral slit. Macronucleus in two spherical to ovoid parts with a single micronucleus between them. 1–3 micronuclei according to Maupas (1883). Macronuclear parts fuse during bipartition (Horváth & Kuhn, 1941) (Figs 38–42) and divide in the later fission stages (Kahl, 1926). Single contractile vacuole at the posterior pole, diameter about 7 µm, with 5–8 pores on the right lateral side (Horváth & Kuhn, 1941) (Fig. 43) which could not be seen in our slides. Cytoproct terminal, a slightly laterally located slit (Maupas, 1883; Kahl, 1926). Pellicle soft, flexible, with longitudinal furrows in which the cilia and bristles originate. Furrows disappear in well-fed individuals. Extrusomes straight to slightly fusiform (arrow-shaped according to Foissner, 1977/78), thin, about 4 µm long (2 µm according to Horváth & Kuhn, 1941), located along the cytostome, a small accumulation of them in the ventral side of the posterior end and even a few scattered throughout the body (Figs 48, 49). Cytoplasm of normally-fed specimens rather clear, containing some small colourless spheres. Carnivorous, feeds on small hymenostome ciliates, e.g. *Colpidium, Cyclidium, Glaucoma, Pseudocohnilembus, Loxocephalus, Uronema* (Maupas, 1883; Lepsi, 1926*a*; Kahl, 1926, 1931; Buck, 1961; Struhal, 1969). Starved individuals feed even on 'cysts' of *Euglena viridis* (Horváth & Kuhn, 1941) and perhaps on bacteria (Lepsi, 1926*a*). Ingestion vacuoles rather large, dividing quickly into smaller food vacuoles (Horváth & Kuhn, 1941). Movement moderately quick, gliding on the bottom of the petri-dish or swimming in rotation along its longitudinal axis. Bipartition by transverse fission (Lepsi, 1926*a*; Horváth & Kuhn, 1941) (Figs 38–42). Opisthe almost spherical when it separates from the proter (Kahl, 1926; Horváth & Kuhn, 1941) (Fig. 40). Very small degenerative forms tend to conjugate; during this process the mouth of an individual fuses with the back of another (Kahl, 1926) (Fig. 20). Encystment frequently occurring when food is depleted (Horváth & Kuhn, 1941). Endocyst forms within an hour, later the macronuclear parts fuse to a worm-shaped product. Wall of ectocyst without visible structure. Cysts surrounded by some material which sticks them to the bottom of the culture dishes or to the bacterial film on the surface of the culture medium (Horváth & Kuhn, 1941) (Fig. 35).

Three different types of cilia: (1) normal cilia, about 10 µm, (2) short bristles, about 0·5–1·0 µm, (3) club-shaped bristles, up to 2·0 µm. Eleven longitudinal kineties with cilia type 1, about 8–9 of them on the right and about 3 on the left side. This is in accordance with the numbers given by Kahl (1926), Horváth & Kuhn (1941), and Fryd-Versavel *et al.* (1975). In addition to the normal somatic kineties the following are found on the more differentiated left side: (1) a single kinety with cilia type 2 located to the left of the brosse kinety and often extending only to the middle of the body, its posterior basal bodies less closely spaced, (2) one brosse row of obliquely arranged, paired bristles (cilia type 3) being posteriorly continued by a row of unciliated kinetosomes (or by kinetosomes



with very short bristles only), (3) one kinety consisting apically of 2–3 cilia of type 3 (probably constituting a rudimentary brosse row) and being continued by a few unciliated kinetosomes (about 5 in the anterior third and about 3 kinetosomes in the middle of the body). Kahl (1926, 1931) described the brosse as being built up of 3 rows of bristles (Fig. 21). Foissner (1977/78) observed only a file-shaped structure there, most probably suggested by the single row of paired brosse-bristles.

Cytostome more or less curved, anteriorly overlapping to the left side but not to the right as described by Lepsi (1926*a*,*b*, 1928). Perioral kinety 1 left of cytostome, with paired basal bodies along the mouth, however, only the anterior basal body each bearing cilia of type 2. Perioral kinety 2 and 3 to the right of the oral slit showing closely spaced basal bodies and constituting the so-called 'mane', a conspicuous compact ciliature. Perioral kinety 2 with paired basal bodies along the oral slit, the anterior basal body bears a cilium of type 1. This kinety appears unciliated post-orally. Perioral kinety 3 with single basal bodies but ciliated along the whole body with cilia type 1. Horváth & Kuhn (1941) misinterpreted the perioral kineties 2 and 3 as left and right perioral kineties. Their drawing, however, shows the correct situation, that is to say also perioral kinety 1 (Figs 43, 44). Fryd-Versavel *et al.* (1975) overlooked the perioral kinety 3 (Figs 45–47).

The silverline system is a linearly orientated fine-meshed lattice (Foissner, 1977/78) (Fig. 50a).

OCCURRENCE AND ECOLOGY. Dujardin (1841) found this species in a 20-day-old infusion of material from the Mediterranean Sea. Later it was recorded from the brackish waters of Oldesloe and Kiel (Kahl, 1928, 1933), from the Roumanian littoral of the Black Sea (Lepsi, 1926*a*,*b*, 1928; Tucolesco, 1962*a*) and from the periphyton of brackish and marine waters of Königshafen near List (Sylt, Germany) (Küsters, 1974).

Some authors mentioned also terrestrial habitats (Radu & Tomescu, 1972; Tomescu, 1978), but a reliable record is not available (Foissner, 1987). The drawing made by Stella (1948), who claimed to have found *Acineria incurvata* in a pine forest, indicates that it was (probably) a member of the genus *Spathidium* (Fig. 22).

Acineria incurvata has been frequently found in strongly saprobic freshwater habitats, such as different sewage-loaded watercourses (Horváth & Kuhn, 1941; Buck, 1961; Bick, 1972; Madoni & Ghetti, 1977; Foissner, 1977/78), in *Sphaerotilus* tufts (Vašiček, 1964; Struhal, 1969), on the bottom of the river Elbe upstream from Hamburg (Grimm, 1968), in a cesspool (Kahl, 1926), and in sewage-treatment plants (trickling filters in good working order, aeration tanks) (Buck, 1961; Weninger, 1971; Madoni, 1981). Fryd-Versavel *et al.* (1975) found their *'Litonotus lamella'* in a pond in the year 1962. Šrámek-Hušek (1956, 1958) noted it as a true member of the 'Colpidietum colpodae'. Weninger (1971) found a decreasing abundance when nitrate or ammonium was added to sewage, whereas phosphate strongly increased its number.

The above data suggest that *Acineria incurvata* is a widely distributed polysaprobic euryhaline indicator species with a rather high tolerance of lack of oxygen and high concentrations of NH_4^+.

Figs 1–23 *Acineria.*

Figs 1, 2 *Acineria incurvata* after Dujardin (1841).

Fig. 3 *Acineria acuta* after Dujardin (1841).

Fig. 4 *Acineria nasuta* after Lepsi (1962).

Figs 5–11 *Acineria uncinata* after Tucolesco (1962*a*). **5** Anterior pole. **6** Posterior pole, **7, 8** Right and left side. **9** Mouth and anterior pole overlapping towards the left side. **10** Ventral view. **11** Dorsal view.

Figs 12–23 *Acineria incurvata.* **12–15** After Maupas (1883). **12** An individual swallowing an *Uronema.* **13** Right side (Maupas called it dorsal view). **14** Left side (Maupas called it ventral view). **15** Pellicle. **16** After Kahl (1931), left side. **17–21** After Kahl (1926). **17, 18** Left side of different individuals. **19** Right side. **20** Conjugants. **21** Left anterior region. **22** After Stella (1948), probably a *Spathidium.* **23** After Buck (1961).

Table 1 Biometrical characterization of *Acineria incurvata*

Character[1]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	56·25	54·5	7·50	1·67	13·3	46·0	75·0	20
Body, width	15·50	16·0	2·01	0·45	13·0	12·0	19·0	20
Number of macronucleus parts	2·00	2·0	0·00	0·00	0·0	2·0	2·0	20
Macronucleus part, length	9·65	10·0	1·60	0·36	16·6	7·0	13·0	20
Macronucleus part, width	7·35	7·5	0·83	0·18	13·3	6·0	9·0	20
Number of micronuclei	1·00	1·0	0·00	0·00	0·0	1·0	1·0	20
Micronucleus, length	2·42	2·2	0·66	0·15	27·1	1·8	4·0	20
Micronucleus, width	2·12	2·0	0·47	0·11	22·3	1·6	3·6	20
Cytostome, length (measured as chord)	22·55	22·0	3·50	0·78	15·5	15·0	28·0	20
Distance from apex to posterior end of brosse	16·90	19·5	2·66	0·60	13·6	14·0	25·0	20
Number of brosse-bristles	41·20	40·0	4·18	0·93	10·1	34·0	48·0	20
Brosse-bristles, maximal length	1·72	1·8	0·24	0·05	14·3	1·2	2·0	20
Number of left perioral kineties	1·00	1·0	0·00	0·00	0·0	1·0	1·0	20
Number of right perioral kineties	2·00	2·0	0·00	0·00	0·0	2·0	2·0	20
Number of normally ciliated kineties (cilia type 1), perioral kineties excluded	10·85	11·0	0·59	0·13	5·4	10·0	12·0	20

[1] All data are based on protargol silver impregnated specimens. All measurements in µm. Legend: $\bar{x}$, mean; M, median; SD, standard deviation; SE, standard error of mean; CV, coefficient of variation in %; Min, minimum; Max, maximum; n, sample size.

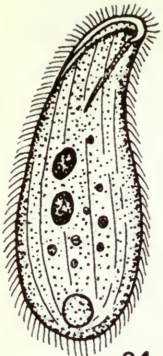
REMARKS. *Trachelius anaticula* Ehrenberg, 1833 is an older but unreliable synonym of this species. *Acineria acuta* Dujardin, 1841, which was observed in the water of a wheel-track in 1838, has been very insufficiently described and therefore cannot be discriminated from *Acineria incurvata*. Thus, *Acineria acuta* is here treated as synonym. *Amphileptus anaticula* perhaps is a synonym, too, but the figure given by Claparède & Lachmann (1859) shows an unidentifiable individual with a voluminous ingestion vacuole. The synonym *Lionotus reversus* Kahl, 1926 results *par lapsus*, since Kahl mentioned in a footnote that he had found Maupas' good description of *Acineria incurvata* just after having finished the manuscript. The synonym *Litonotus lamella* results from an obvious misidentification by Fryd-Versavel *et al.* (1975).

Acineria nasuta Lepsi, 1962

DIAGNOSIS (Fig. 4). Marine. About 90–100 µm long, rather wide. Only one single macronucleus. Pellicle with 5–6 distinct stripes. Postapical, to the right of the so-called 'nose' a peculiar line (perhaps the mouth) which is said to be characteristic of this species.

OCCURRENCE AND ECOLOGY. Only a few individuals were found in a raw culture of putrefying marine algae. In the same culture *Holophrya torquabilis* occurred in large numbers, probably serving as food for *Acineria*.

Figs 24–47 *Acineria incurvata*. **24–30** After Lepsi (1965). **24** Normal aspect. **25** *Trachelius*-like form. **26** Slender form, resembling *Spathidium*. **27** Degenerated individual resembling *Litonotus*. **28–30** Abnormal, degenerated forms. **31–44** After Horváth & Kuhn (1941). **31–34** Outlines of well-fed and starved specimens. **35** Cyst. **36** Left side, with extrusomes along the cytostome. **37** Right side, location of contractile vacuole and of kineties. **38–42** Bipartition. **43, 44** Infraciliature (right and left side) revealed by Bresslau's opalblue-technique. **45–47** After Fryd-Versavel *et al.* (1975), misidentified as *Litonotus lamella*. **45, 46** Infraciliature of left and right side. **47** Diagram of different types of cilia and bristles in the anterior region.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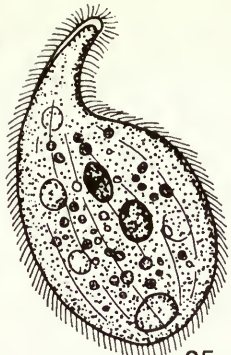
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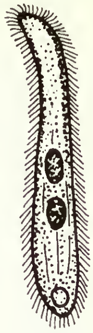
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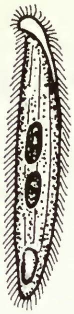
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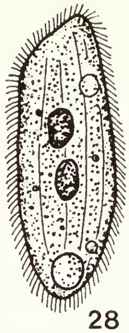
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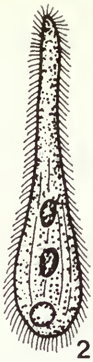
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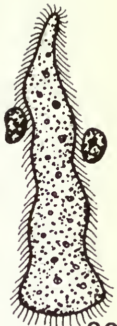
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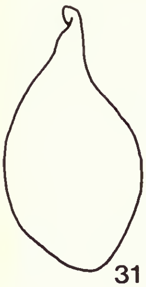
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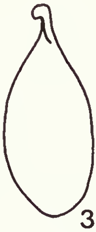
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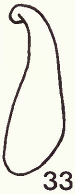
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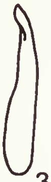
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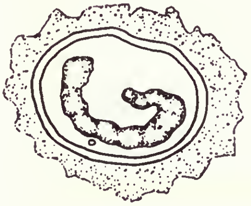
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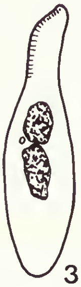
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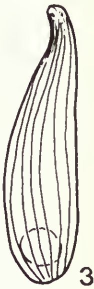
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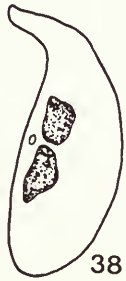
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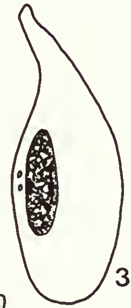
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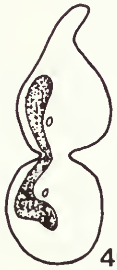
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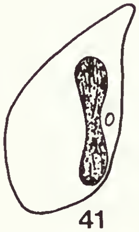
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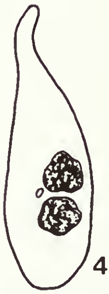
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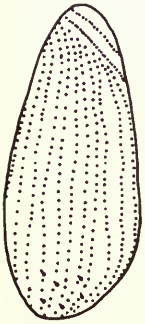
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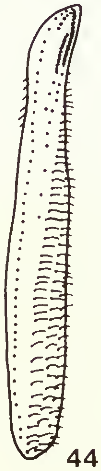
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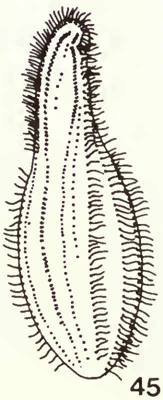
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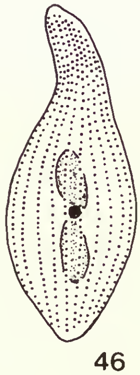
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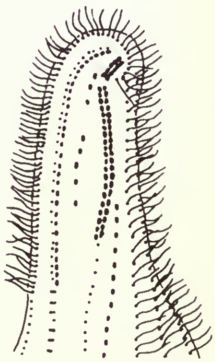
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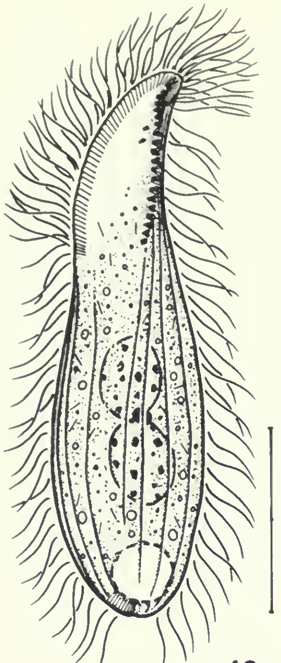

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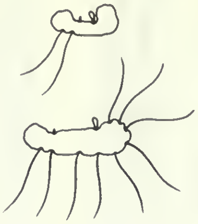

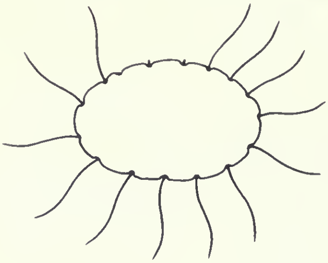

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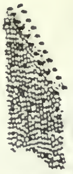

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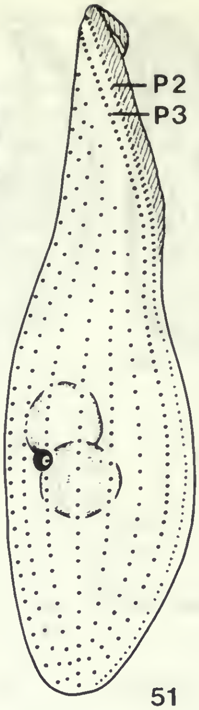

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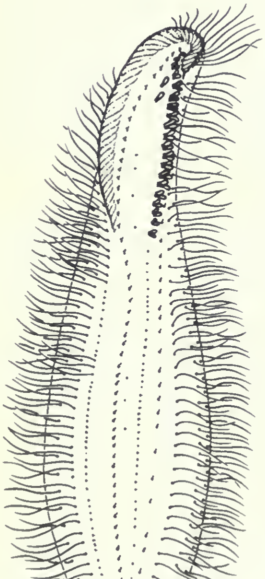

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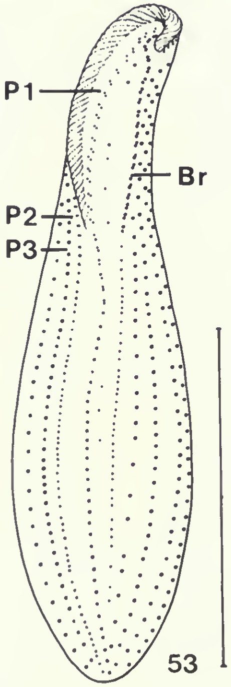

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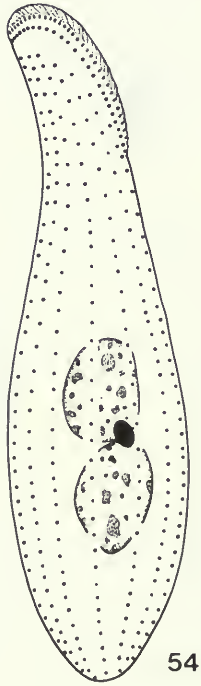

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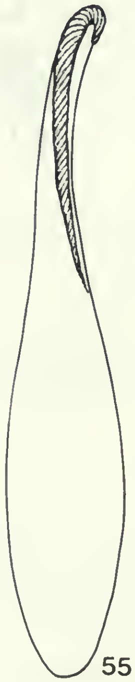

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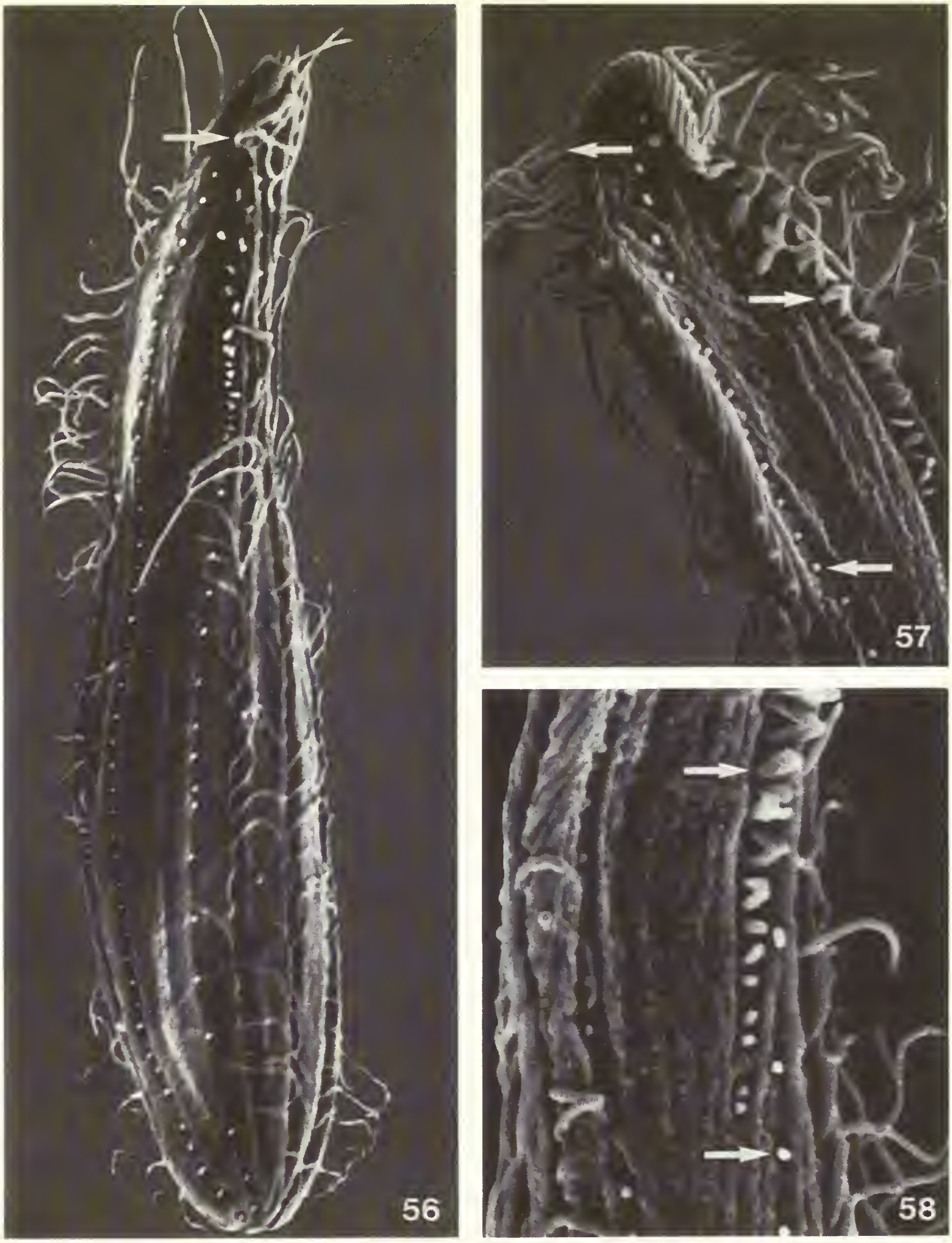

Figs 56–58 *Acineria incurvata*, scanning electron micrographs. **56** Total view of left side. **57** Anterior part with dorsal oral region rolled up forming a spoon-like excavation. Note the club-shaped brosse-bristles, the short bristles of the perioral kinety 1, and the long cilia of perioral kineties 2 and 3 (arrows). **58** Detail of anterior third with brosse-bristles, short bristles and normal cilia (arrows).

Figs 48–55 *Acineria incurvata*, originals. **48** Left side from life and according to scanning electron microscopic observations, scale = 20 µm. **49** Extrusome, length about 4 µm. **50** Reconstructed cross-sections in different regions of body. **50a** Silverline system in the oral region, dry silvered, after Foissner (1977/78). **51** Right side, infraciliature of a protargol silver stained specimen. P2, P3, perioral kineties 2 and 3. **52** Left ventro-lateral view of a protargol silver stained specimen with different types of cilia and bristles according to SEM-observations. **53, 54** Infraciliature of the left ventro-lateral and the right dorso-lateral side of a protargol silver impregnated specimen. P1–3, perioral kineties 1–3; Br, Brosse; scale = 30 µm. **55** Ventral view.

REMARKS. Lepsi (1962) assumed that this species, which has remained unmentioned since original description, could be a form of *A. incurvata* and mentioned some relationship with the genera *Chilophrya* and *Plagiocampa*. His figure and description are so incomplete that it is at present impossible to find any reliable affinity. The single macronucleus suggests that it is not an Amphileptidae, although he could have observed a dividing stage with fused macronucleus.

Acineria uncinata Tucolesco, 1962*a*

DIAGNOSIS (Figs 5–11). Brackish and freshwater. About 35–55 µm. Body lanceolate without lateral edge. Anterior pole overlapping towards the left side. Two spherical macronuclei showing a clearer zone at their central region. Sometimes a single, elongated, tapered nucleus. Contractile vacuole terminal, often surrounded by a group of smaller vacuoles. Cytostome a straight and short slit restricted to the rolled up anterior pole. Can therefore feed only on small prey (flagellates). Three somatic kineties on the right side with 20–22 cilia each. Cilia at the ventral margin of the anterior third transformed to regularly curved crotchets.

OCCURRENCE AND ECOLOGY. This species was found in summer 1954 in a small dirty brackish puddle near Lake Tekirghiol and in mesosaprobic freshwaters of Bucarest.

REMARKS. Tucolesco (1962*a*) separated this species from *A. incurvata* by the non-overlapping post-oral dorsal margin. However, in *A incurvata* the situation is rather similar (page 199). Thus, we propose the following characters for discrimination from *A. incurvata*: the presence of only three somatic kineties on the right side, the (probably) unciliated left side, and the short oral slit being restricted to the anterior pole. Unmentioned since description. Note after proof reading: This is a valid species which we rediscovered recently! Redescription is in preparation.

Genus ***TRIMYEMA*** Lackey, 1925

Sciadostoma Kahl, 1926

DIAGNOSIS. Trimyemidae Kahl, 1933 (syn. Sciadostomatidae Kahl, 1926) with vestibulum and cytostome near apical end. Vestibular ciliature consisting of three rows of cilia, two rather long ones arranged approximately in a semicircle at the left margin of the vestibulum and an inner rather short third row located near the cytostome at the posterior left of the vestibulum. Somatic ciliature in longitudinal kineties but arranged in a way that a more or less wide band of oblique spirals is formed. Prominent caudal cilium. Body small, mostly tapered at both ends. Free-living and endocommensally, freshwater and marine, polysaprobic.

TYPE-SPECIES. *Trimyema compressa* Lackey, 1925

REMARKS. There is much confusion about the exact orientation of the cell: dorsal, lateral, and ventral sides are often mixed up in descriptions. In addition some authors have given incorrect figures focusing the microscope on the lower surface of their specimens. Thus, they attained inverted figures (see explanations to figures). Most species of the genus *Trimyema* are only superficially described. The oral structures are known exactly only of *T. compressa* (Figs 83, 107) and

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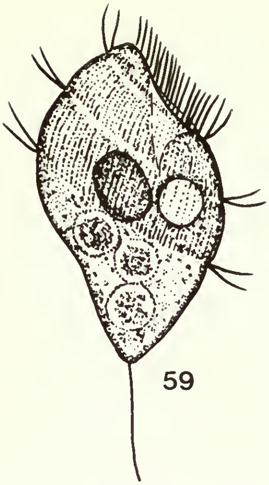
Figs 59–76 *Trimyema compressa*. **59** After Lackey (1925) (inverted). **60** After Wang & Nie (1935), left lateral view. **61–65** After Liebmann (1936). **61** Left ventro-lateral view. **62–65** Defecation by the aid of the caudal cilium. **66–69** After Kahl (1926). **66** Left lateral view. **67** Oral region during progressed bipartition. **68** Ventral side. **69** Bipartition. **70** After Kahl (1931), constant marine form, rather similar to *T. claviformis* described later. **71** After Kahl (1933), left lateral view. **72** After Pennak (1953) (inverted). **73** After Bick (1972), left lateral view. **74** After Sládeček (1972), left lateral view. **75, 76** After Schmall (1976), infraciliature of protargol silver stained specimens (inverted), ventral and dorsal view (Schmall called it dorsal and ventral view).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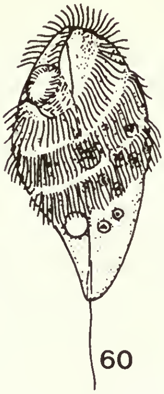
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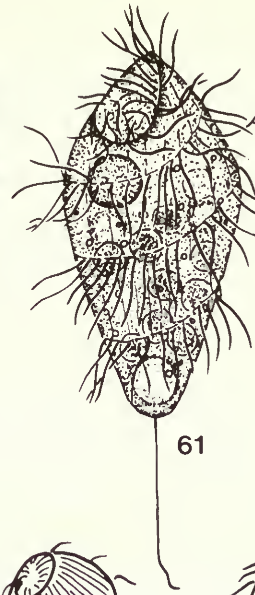
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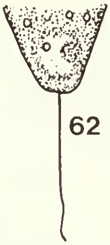
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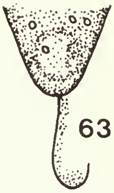
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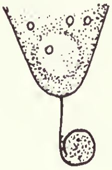
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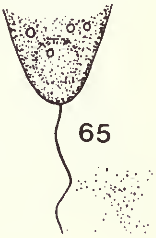
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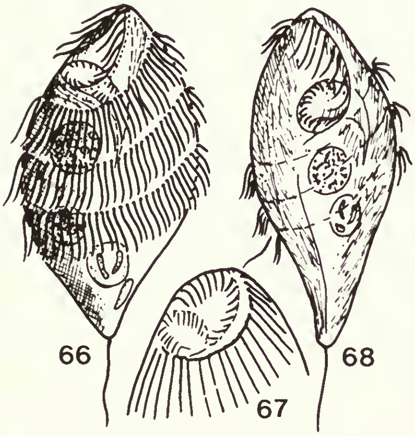
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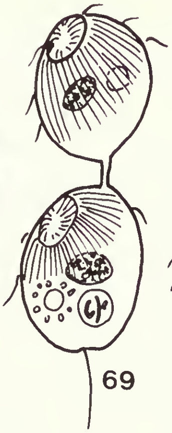
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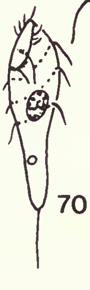
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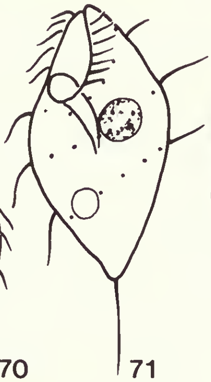
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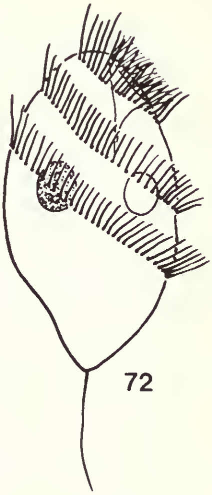
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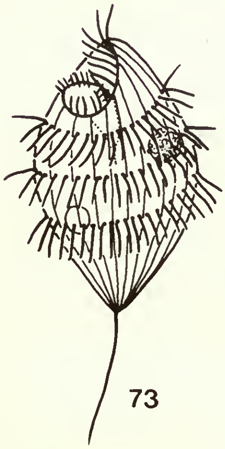
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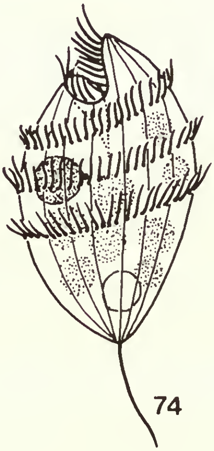
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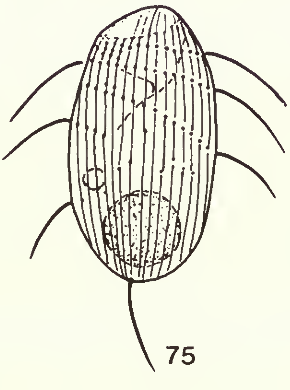
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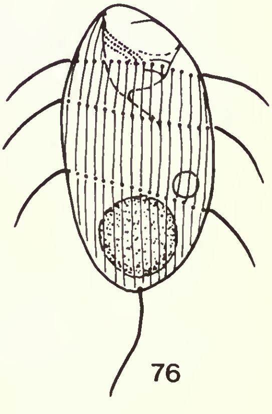
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partly of *T. pleurispiralis* (Fig. 96) and *T. echinometrae* (Fig. 93). From the descriptions and our investigations we deduced the basic structure of the oral apparatus as described above (compare Fig. 107). Fauré-Fremiet (1962) and Borror (1972) obviously overlooked the short third vestibular kinety. Borror (1972) described only an inner and an outer 'polykinety'. Detcheva *et al.* (1981), however, showed in *T. compressa* electronmicroscopically that, despite their polykinetal appearance, the vestibular ciliary systems are not separate polykineties but are the anterior parts of the somatic kineties that are preceded by parasomal sacs and retain the same fibrillar systems as the somatic kinetosomes. Jankowski (1964*a,b*) gave no evidence for his statement that there were four vestibular kineties in *T. compressa.*

Encystment is unknown in this genus. Czapik (1975*a*) noted that even starved specimens (of *T. compressa*) die without forming cysts. Morphogenesis has not yet been exactly studied. However, the oral apparatus is supposed to reduce before cell division, because during division both proter and opisthe show the same state of development of the oral apparatus (Kahl, 1926) (Figs 67, 69).

The silverline system has been demonstrated only in *T. compressa* (Klein, 1930; Fauré-Fremiet, 1962; Jankowski, 1964*a,b*; Czapik, 1975*a*). Klein (1930) gave the description that best agrees with our observations (Figs 106, 110). But he did not draw the transverse silver lines connecting the longitudinal lines in the region of the ciliary spirals. The granules located at and in the silverlines (Fig. 110) have been said to be mucocysts ('Relationskörner') or rudimentary basal bodies (Klein, 1930). However, the electronmicroscopic investigation shows only mucocysts (Detcheva *et al.*, 1981).

The exact taxonomic position of the genus is still unclear. Kahl (1926) created a new family for the rather special helical ciliature. This author, Corliss (1979), and Curds (1982) included the family in the order Trichostomatida Bütschli, 1889. Fauré-Fremiet (1962) noted that the family Trimyemidae indeed presents one of numerous possibilities existing in the order to use the anteriormost somatic kineties for building up a vestibular ciliature. In addition, he indicated possible affinities of *Trimyema* with *Mycterothrix* and *Maryna*, which are now 'good' colpodids (Foissner, 1985*a*). Jankowski (1980) erected the new order Trimyemida (*incertae sedis*) giving no reasons for this decision. On the contrary, Detcheva *et al.* (1981) stated that *Trimyema* is a member of the Vestibulifera and that the Trimyemidae show the same general type of vestibular architecture as the Plagiopylidae and the Coelosomidae. However, a more reasonable classification demands further investigations especially on the morphogenetic processes.

Ruinen (1938) is wrong in transferring *Palmarium salinum* Gajevskaja, 1925 to the genus *Trimyema*, since *Palmarium* is illustrated as having an adoral zone of membranelles (Figs 97–101) (Borror, 1972).

Trimyema pura (Ehrenberg) is listed by Curds (1975) as a species occurring in percolating filters and in activated sludge. We suppose that this species has been described as *Trichoda pura* Ehrenberg, 1831, which according to Corliss & Dougherty (1967) is a synonym of *Tetrahymena pyriformis.*

Lackey (1925) classified *Trimyema* as female using the latin ending -a for his species *T. compressa*. Since we could not find any greek word comparable to 'myema' from which the name of the genus and its sex could be derived we accept Lackey's proposal of the sex. This, however, requires the endings of *T. claviforme*, *T. marinum*, *T. minutum*, and *T. pleurispirale* to be emended (see below).

Key to the species

1a	3 somatic ciliary spirals	2
1b	Usually more than 3 somatic ciliary spirals	3
2a	Posterior end of body tapered, length 25–65 µm	***T. compressa***
2b	Posterior end of body broadly rounded, prominent beak-like pharynx opening, length *c.* 20 µm	***T. minuta***
3a	Body broadly oval, width *c.* half length of body.	4
3b	Body rather slender, fusiform or oblong, width much less than half length of body	5

4a 4(–6) somatic ciliary spirals restricted to the anterior half of body, length *c.* 20–45 µm . . . . *T. pleurispiralis*
4b 7 somatic ciliary spirals restricted to the anterior half of body, length *c.* 25–40 µm, endocommensally in sea-urchins . . . . *T. echinometrae*
5a Body club-shaped, thickened in the anterior region and slender in the posterior region, length *c.* 40 µm, (not totally reliable species!) . . . . *T. claviformis*
5b Body not club-shaped 6
6a Shape of body obviously asymmetric, tapered at both ends, anterior pole bent to the right, posterior pole bent to the left, peristome measures *c.* one third of cell length . . . *T. kahli*
6b Shape of body symmetrical, slender fusiform to slender oblong 7
7a Body length *c.* 40 µm, peristome measures *c.* one fourth of body. . . . . . *T. marina*
7b Body length *c.* 60 µm, peristome measures less than one fourth of body (not totally reliable species!) . . . . *T. alfredkahli*

Descriptions of species

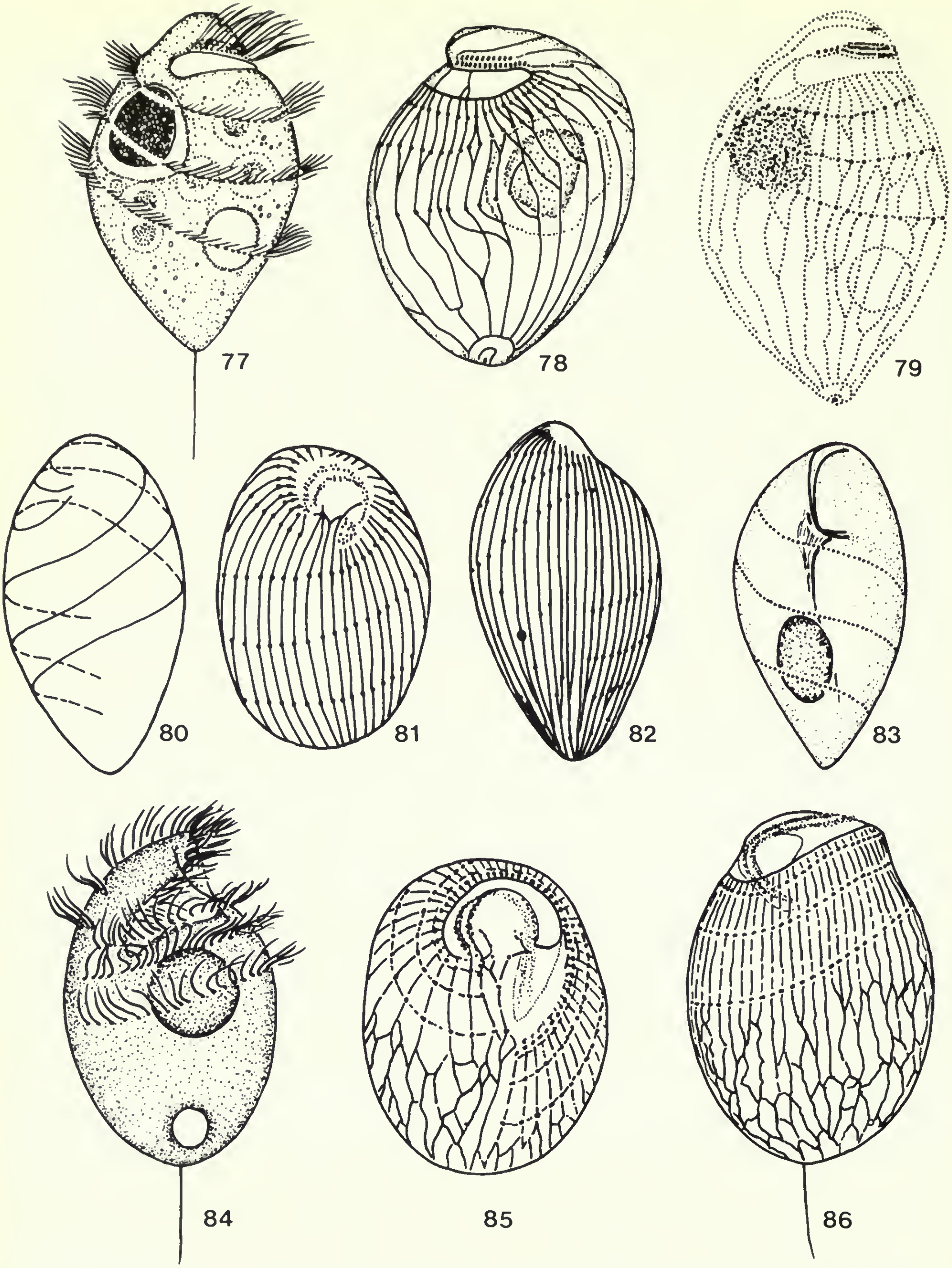
Trimyema compressa Lackey, 1925

Sciadostoma difficile Kahl, 1926
Trimyema compressum Kahl, 1933
Trimyema marinum Fauré-Fremiet, 1962

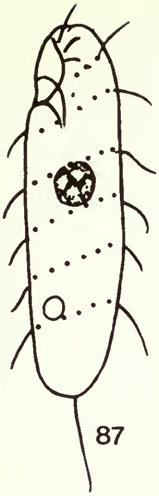
NEOTYPE-SPECIMENS. Slides (dry silvered and protargol silver impregnated) of neotype-specimens have been deposited in the British Museum (Natural History) in London, reference numbers 1986:5:30:2–3.

REDESCRIPTION (Figs 59–86, 104–113, Table 2). Type species of the genus. Freshwater and marine. *In vivo* about 25–50(–60) × 15–20(–35) µm (Lackey, 1925; Kahl, 1926, 1928, 1931, 1933; Wang & Nie, 1935; Liebmann, 1936; Czapik, 1975*a*; Schmall, 1976; Detcheva *et al.*, 1981). Body fusiform to plump S-shaped, laterally slightly flattened, anterior and posterior end slightly tapered. Dorsally and ventrally an inconspicuous ectoplasmatic ridge, the so-called keel (unrecognized by us) (Kahl, 1926; Wang & Nie, 1935). Macronucleus spherical to slightly oval, located centrally in most specimens. Schmall (1976) found it to be more variable, also located posteriorly. Micronucleus closely attached to the macronucleus. In protargol impregnated specimens often a second, weakly stained macronucleus-like structure, probably a large ingestion vacuole (Fig. 109). Macronucleus usually heavily stained, surrounded by dark, slightly curved rods measuring *c.* 2 µm in length and 0·5 µm in width. These aggregated rods look like bacteria. Detcheva *et al.* (1981), however, consider them to be mitochondria, which is not supported by recent studies on other sapropelic ciliates (Van Bruggen *et al.*, 1984). Contractile vacuole and its pore located in the region of the last ciliary spiral on the right ventro-lateral side. Cytoproct a slit *circa* 5–10 µm long, located in the right dorso-lateral surface (Figs 104, 105, 108). Pellicle thin, flexible and deformable, with very slight ridges paralleling the longitudinal kineties. In protargol impregnated specimens these ridges appear darkly stained and produce a negative image of the silverline system. Cytoplasm rather transparent, contains a lot of refractive long-oval (length about 0·5–1·5 µm) granules which are also visible in protargol stained specimens. They are most probably the mucocysts described by Detcheva *et al.* (1981). Food vacuoles about 5 µm in diameter. Cyclosis pronounced (Lackey, 1925). Feeds on bacteria but is not dependent on sulphur bacteria (Liebmann, 1947). Moves slowly and slightly tremblingly in a straight line or in the arc of a circle rotating on its longitudinal axis (Lackey, 1925). Reproduction by transverse fission (Lackey, 1925; Kahl, 1926, 1931; Czapik, 1975*a*).

Somatic cilia 7–9 µm, strongly beating, arranged in about 50–60 longitudinal kineties but more commonly viewed as 3 oblique spirals. In the anterior region of these spirals the third, fourth, and fifth kinetosomes are paired, constituting the compact field of cilia, consisting of 3 × 4 and 2 × 2 cilia, described by Schmall (1976) (Figs 75, 113). A short row of about 5–10 cilia on the ventral side extends obliquely from the posterior end of the anteriormost somatic spiral to the right. Posterior



Figs 77–86 *Trimyema compressa*. **77–79** After Jankowski (1964). **77** From life (inverted). **78** Left lateral view of a dry silver impregnated specimen. **79** Lateral view of a dry silvered specimen (inverted). **80–82** After Czapik (1975*a*), specimens stained by Chatton's method as modified by Corliss. **80** Scheme representing the disposition of the ciliary spirals. **81** Ventro-apical region. **82** Ventral side (Czapik called it right side). **83** After Detcheva *et al.* (1981), dorsal view (inverted). **84–86** After Fauré-Fremiet (1962) who identified it erroneously as *T. marina*. **84** From life. **85** Apical view of Chatton-Lwoff impregnated specimen. **86.** Infraciliature and silver lines of left dorso-lateral side of a Chatton-Lwoff impregnated specimen (Fauré-Fremiet interpreted it as left ventro-lateral view).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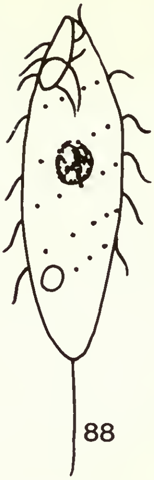
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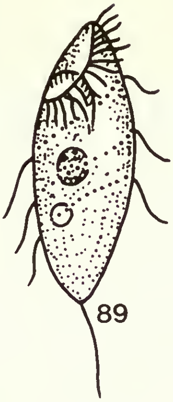
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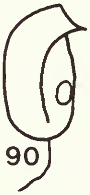
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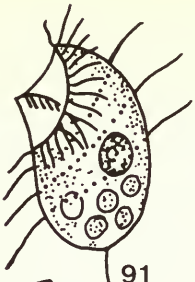
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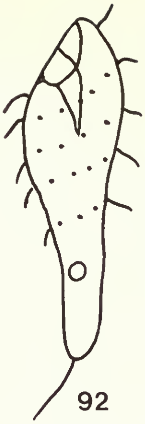
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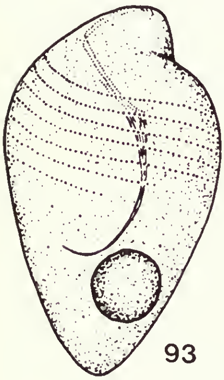
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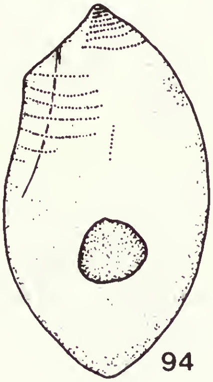
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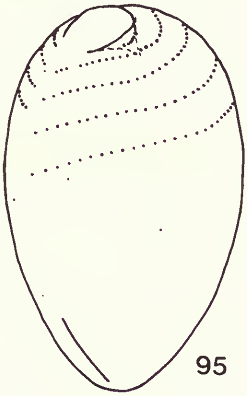
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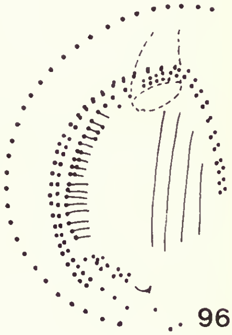
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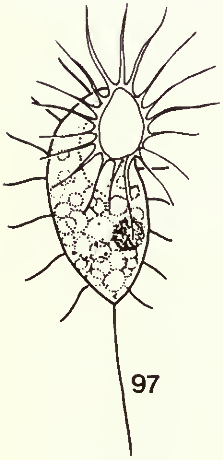
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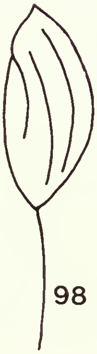
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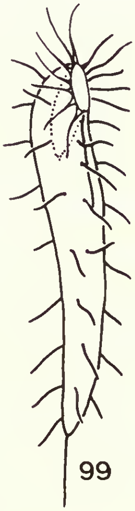
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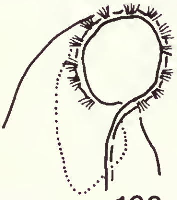
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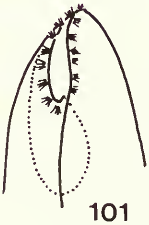
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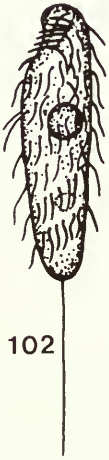
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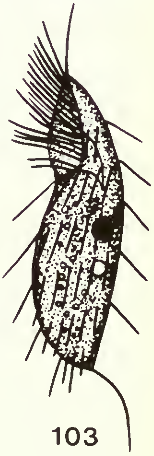
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third of body unciliated apart from the caudal cilium measuring about one third to one half of body length (Lackey, 1925; Kahl, 1931; Wang & Nie, 1935); it is perhaps involved in the process of defecation (Liebmann, 1936) (Figs 62–65).

Vestibulum *circa* one third of body length, funnel-shaped. Left half of the oral depression more excavated than the right one and, as a consequence, the left margin becomes a thin, transparent layer of ectoplasm and forms a cap or hood-like process bordering the vestibulum (Kahl, 1926; Wang & Nie, 1935). Cytopharyngeal fibres inconspicuous, rectangular to the entrance of the vestibulum. Vestibular kinety 1 a bit longer than vestibular kinety 2. At their anterior ends 4 to 5 pairs of basal bodies or single basal bodies with parasomal sacs. Vestibular kinety 3 consists of only 6–7 cilia (Figs 107, 111, 112). In stained specimens somatic as well as vestibular kinetosomes appear to be paired (Figs 106–113) but in fact, the anterior granule is a parasomal sac (Detcheva *et al.*, 1981), probably with the exception of the above mentioned compact field.

About 60 longitudinal silver lines (Czapik, 1975*a* mentioned 52 lines), connected by transverse lines which are located between the somatic ciliary spirals. In front of the anteriormost ciliary spiral a circumoral silver line from which a few longitudinal lines extend to the vestibulum forming square-like fields at its rim. The longitudinal silver lines fuse at the posterior third forming rough meshes (Figs 106, 110).

OCCURRENCE AND ECOLOGY. First recorded from the sewage disposal of Imhoff tanks in New Jersey and later listed as an obligate anaerobe (Lackey, 1925, 1938; Noland & Gojdics, 1967). Very similar habitats were reported by Liebmann (1936, 1947, 1951), who found *T. compressa* regularly in waters containing a lot of organic matter and H_2S, such as in over-loaded percolating filters, in Imhoff tanks (3–5 ind.ml^{-1} and 40 ind.ml^{-1}), in sewers, and at the outfalls of communal waste waters.

Further habitats are the sapropel of ponds near Leningrad (Jankowski, 1964*a,b*), ponds used for the treatment of sugar factory wastes (Grabacka, 1973), the plankton of the eutrophic pond 'Poppelsdorfer Weiher' in Bonn (Wilbert, 1969), a small eutrophic lake at Uttendorf/Salzburg (Foissner, unpublished), and an arctic tundrapond at Barrow/Alaska (Fenchel, 1975). Detcheva (1972) and Czapik (1975*a,b*) listed up Bulgarian and Polish habitats like ponds, lakes, ditches, and polluted rivers. Wang & Nie (1935) observed some individuals among decaying organic substances taken from Lake Ho Hu. Kahl (1926, 1931, 1933) found it in the sapropel, in a cesspool, in sewage, and more rarely in the brackish waters of Oldesloe (Kahl, 1928) thus considering it to be of freshwater origin. Fauré-Fremiet (1962) found it in a rock pool on the French Atlantic coast. Tucolesco (1962*b*) recorded it from the Black Sea and from the saliferous, para-marine Lake Tekirghiol in Roumania. According to Sládeček (1972) *T. compressa* developed in great numbers (up to 10,000 ind.ml^{-1}) in a sample of industrial waste water from a textile factory.

Figs 87–103 *Trimyema.*

Figs 87–89 *Trimyema marina.* **87, 88** After Kahl (1933). **89** After Kahl (1931).

Figs 90, 91 *Trimyema minuta* after Kahl (1931), dorsal and left lateral view.

Fig. 92 *Trimyema claviformis* after Kahl (1933).

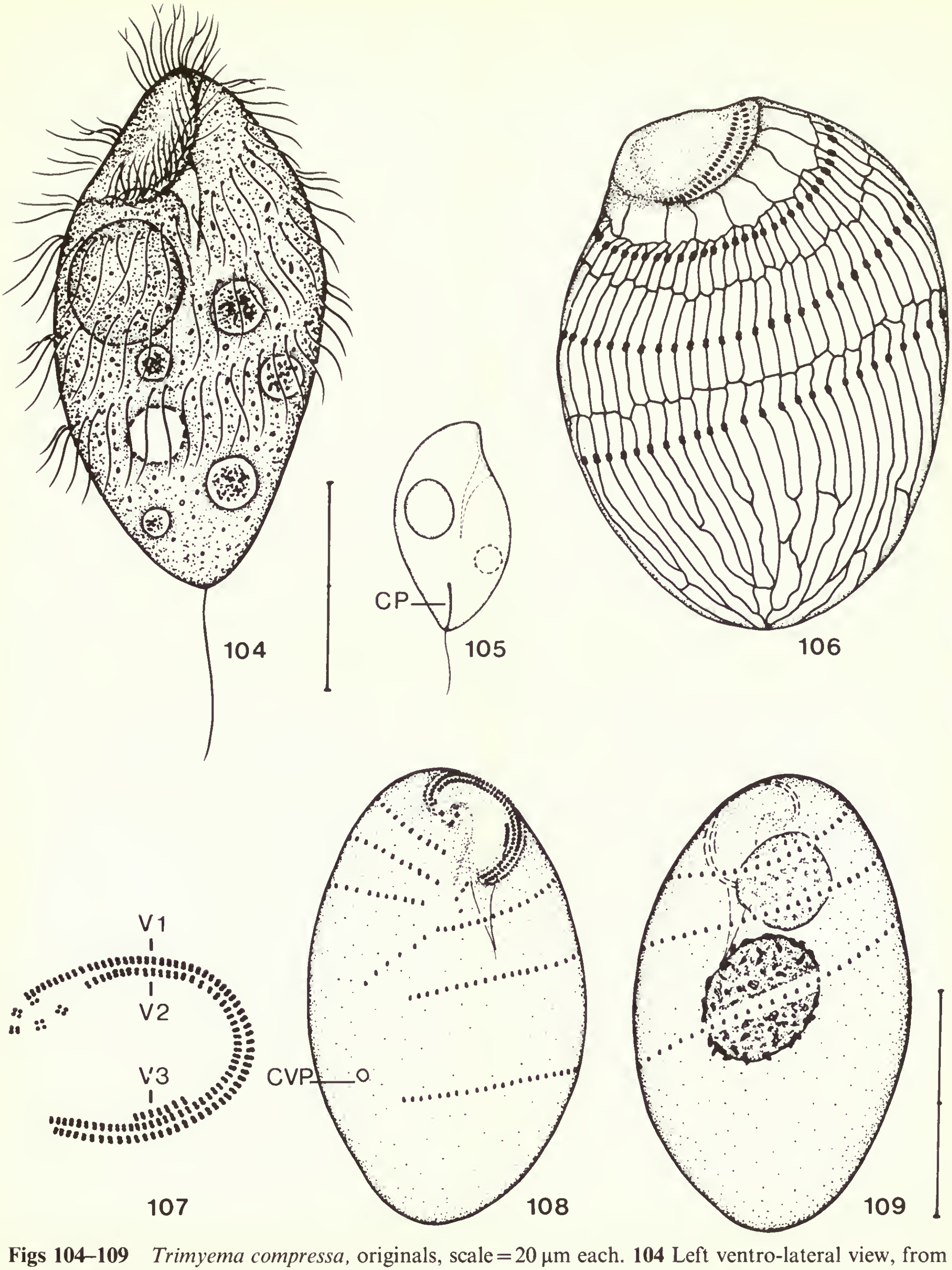
Figs 93, 94 *Trimyema echinometrae* after Grolière *et al.* (1980), protargol silver impregnated specimens (inverted), lateral view and ventral view (the latter designated as lateral view, too).

Figs 95, 96 *Trimyema pleurispiralis* after Borror (1972). **95** Left ventro-lateral view. **96** Anterior pole with anteriormost somatic ciliary spiral (at the left) and with vestibular ciliature.

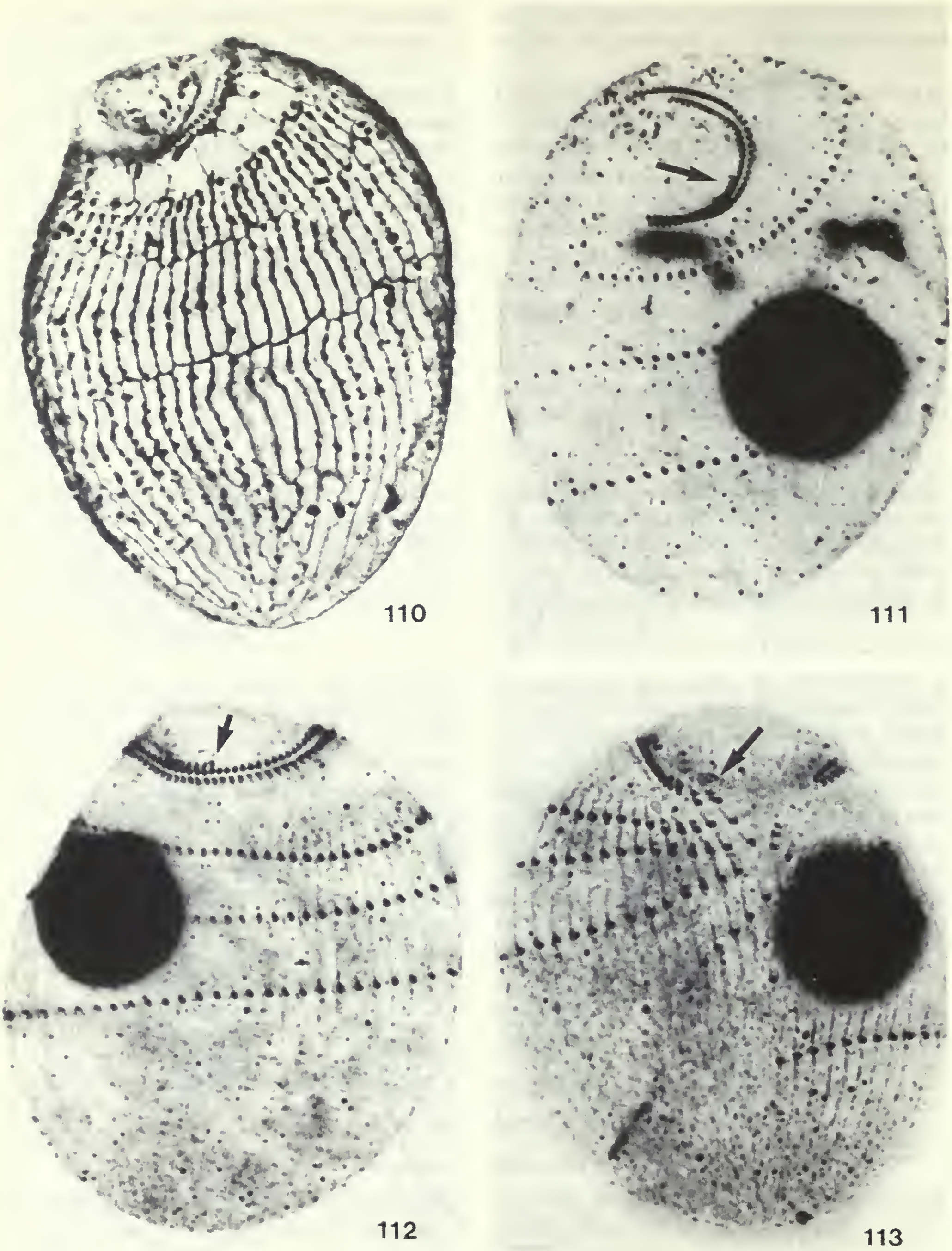
Figs 97–101 *Palmarium salinum* Gajevskaja after Ruinen (1938). **97, 98** Normal form, ventral and dorsal view. **99** Slender (abnormal?) form. **100, 101** Peristome, ventral and lateral view.

Fig. 102 *Trimyema alfredkahli* after Tucolesco (1962*a*), left lateral view.

Fig. 103 *Trimyema kahli* after Tucolesco (1962*a*), left lateral view.



Figs 104–109 *Trimyema compressa,* originals, scale = 20 µm each. **104** Left ventro-lateral view, from life. **105** Right dorso-lateral view of an S-shaped individual. CP, cytoproct. **106** Dorsal view of a dry silvered specimen. **107** Vestibular ciliature revealed by Fernandez-Galiano's method. The shape of the vestibular kineties has been slightly deformed by preparation; they are less curved in life. V1–3, vestibular kineties 1–3. **108, 109** Ventral and dorsal view of a protargol silver impregnated specimen amended with details from individuals impregnated with Fernandez-Galiano's method. CVP, contractile vacuole pore.



Figs 110–113 *Trimyema compressa.* **110** Silverline system revealed by the dry silver impregnation technique, dorsal view. **111–113** Specimens stained by Fernandez-Galiano's impregnation technique. **111** Left side with the three ciliary spirals and apex with vestibular ciliature consisting of two long rows and one short row of cilia (arrow). **112** Dorsal view, arrow indicates the three vestibular kineties. **113** Ventral view, arrow indicates the isolated basal bodies at the anteriormost region of the vestibular kineties.

Bick (1968, 1972) gave the most detailed ecological characterization. *T. compressa* is an outstanding indicator of polysaprobity (Liebmann, 1951), isosaprobity and even metasaprobity (Sládeček, 1973) and occurs in waters receiving fresh manure and sewage, or waste waters containing cellulose material (paper mill outlets, etc.). The species seems to prefer conditions with low ammonia content, i.e. conditions prevailing during the decay of cellulose and other material poor in nitrogenous compounds. The saprobiological evaluation is indicated by Sládeček (1972): $x=0$, $o=0$, $\beta=0$, $\alpha=0$, $p=10$, $G=5$, $s=5{\cdot}3$ (E, H_2S).

Remarks. This species differs from *T. minuta* particularly by the tapered posterior end. It can easily be distinguished from the other species by its having only three somatic ciliary spirals. Fauré-Fremiet (1962) observed an abundant population of *Trimyema* (Figs 84–86) and identified it as *T. marina* although it was of an ovoid and stocky form which was not described by Kahl (1931, 1933, 1935). On the contrary this author later stated that *T. marina* is usually one third to one half more slender than he drew it in 1931 (Kahl, 1931, Fig. 89; Kahl, 1933, Figs 87, 88). Thus we suppose that Fauré-Fremiet worked on *T. compressa*.

Table 2 Biometrical characterization of *Trimyema compressa*

Character[1]	x̄	M	SD	SE	CV	Min	Max	n
Body, length	39·05	39·5	4·58	1·03	11·7	32·0	47·0	20
Body, width	22·30	23·0	3·01	0·67	13·5	17·0	26·0	20
Macronucleus, length	11·05	11·0	1·57	0·35	14·2	9·0	14·0	20
Macronucleus, width	9·35	9·5	1·50	0·34	16·0	6·0	12·0	20
Number of vestibular ciliary rows	3·00	3·0	0·00	0·00	0·0	3·0	3·0	20
Number of somatic ciliary rows	3·00	3·0	0·00	0·00	0·0	3·0	3·0	20
Number of caudal cilia	1·00	1·0	0·00	0·00	0·0	1·0	1·0	20
Distance from apex to posterior end of vestibulum	9·80	10·0	1·88	0·42	19·2	7·0	15·0	20
Distance between posterior end of body and posterior end of ciliary spirals	11·00	11·0	1·78	0·40	16·2	7·0	15·0	20

[1] See footnote Table 1

Trimyema alfredkahli Tucolesco, 1962*a*

Diagnosis (Fig. 102). Marine. About 60 μm. Body oblong and slender, slightly tapering anteriorly and posteriorly. Oral apparatus particularly small, bounded at the right margin by a conspicuous dilatation. Macronucleus spherical. Cilia long and fine. According to Tucolesco's figure ciliary spirals cover nearly the whole body, which contrasts his description. Caudal cilium longer than half body length.

Occurrence and ecology. Found in an abundant population in a mixed polysaprobic culture taken from the Black Sea in March 1955.

Remarks. This species has remained unmentioned since description. It can perhaps be distinguished from *T. marina* by its oblique orientation of the oral apparatus, which is stressed by Tucolesco (1962*a*), and by its larger size. However, synonymy cannot be excluded.

Trimyema claviformis Kahl, 1933

Trimyema claviforme Kahl, 1933

Diagnosis (Fig. 92). Marine. *Circa* 40 μm. Body club-shaped. Posterior third of body unciliated.

Occurrence and ecology. Found in sapropelic habitats of Sylt and Kiel (Germany).

REMARKS. Very insufficiently described. With exception of the unciliated tapering posterior third of body identical with *T. marina*. Even Kahl (1935) noted that he established this species with some doubt. Thus, synonymy cannot be excluded.

Trimyema echinometrae Grolière, Puytorac & Grain, 1980

DIAGNOSIS (Figs 93, 94). Marine. Living endocommensally in sea-urchins. About 31 (27–40) × 17 (13–20) µm. Body peg-top like. Macronucleus spherical, 5–7·5 µm in diameter, posteriorly located. Micronucleus not visible. 60 to 70 longitudinal somatic kineties. Cilia distributed in 7 parallel spirals in the anterior half of body. Three vestibular kineties very similarly arranged as in *T. compressa*.

OCCURRENCE AND ECOLOGY. Found in the sea-urchins *Diadema antillarum* and *Echinometra lucunter* from the Gulf of Mexico and the Gulf of Guadeloupe. Housing together with other commensal species like *Biggaria echinometris, Metanophrys elongata* and *Metopus circumlabens* (Grolière *et al.*, 1980). Perhaps already Profant (1966) observed this species, since he mentioned *Trimyema sp.* to be a ciliate inhabiting echinoids in the Eastern Pacific Ocean.

REMARKS. *T. echinometrae* is a reliable species. It differs from the other members of the genus in the number of ciliary spirals. The figures, however, are obviously inverted, because in the genus *Trimyema* the spirals run the other way round. Furthermore, the identification is impeded by the missing drawing from life.

Trimyema kahli Tucolesco, 1962*a*

DIAGNOSIS (Fig. 103). Para-marine. About 36–40 µm. Body conspicuously asymmetric, inverted S-shaped. Peristome in the anterior third of body. Macronucleus spherical, usually located in the middle of the cell. Contractile vacuole close behind the middle of body. Cilia long and fine. Ciliary spirals extending to the posterior pole. Caudal cilium almost rigid, bent to the left.

OCCURRENCE AND ECOLOGY. Polysaprobic, found constantly in the para-marine Roumanian Lake Tekirghiol (Tucolesco, 1962*a,b*).

REMARKS. This species has remained unmentioned since 1962. However, from its general appearance it seems to be a reliable but insufficiently described species.

Trimyema marina (Kahl, 1931)

Sciadostoma marinum Kahl, 1931
Trimyema marinum Kahl, 1933

DIAGNOSIS (Figs 87–89). Marine. About 40 µm. Slender fusiform to slender oblong (4 : 1). In the original figure (Fig. 89) similar to *T. compressa* but later figured and redescribed with 5–6 ciliary spirals (Figs 87, 88).

OCCURRENCE AND ECOLOGY. Repeatedly observed in putrid water of the North and East Sea (Sylt, Kiel) and in salt-water from Oldesloe (Kahl, 1931, 1933, 1935).

REMARKS. Kahl (1931) considered *T. marina* to be a separable species because he never found similar forms among numerous populations of the freshwater form of *T. compressa*. Later he thought that two forms of this species probably exist and erected the species *T. claviformis* (Kahl, 1933) which, however, is not a totally reliable species (Kahl, 1935). We consider this species and *T. alfredkahli* perhaps to be junior synonyms of *T. marina*.

Trimyema minuta nov. comb.

Sciadostoma minutum Kahl, 1931

DIAGNOSIS (Figs 90, 91). Freshwater and marine. About 20 µm. Rounded posterior and a prominent beak-like pharynx-opening. Ectoplasmatic ridge (keel) more pronounced than in *T.*

compressa, extending from the beak-like pharynx-opening over the back to the posterior. Cilia longer and more rigid than in *T. compressa.*

OCCURRENCE AND ECOLOGY. This species was found together with *T. compressa* and was first considered as a modification, but once an abundant population occurred in a ditch contaminated with liquid manure (Kahl, 1931). Wenzel (1961) observed *T. minuta* in the sponge *Halichondria panicea* from the Gulf of Naples. Tucolesco (1962*b*) recorded it twice from old, mixed infusions of the para-marine Roumanian Lake Tekirghiol.

REMARKS. Kahl (1931) doubted the species status of this form and did not mention it again in his publication of the year 1935. Further investigations are necessary.

Trimyema pleurispiralis Borror, 1972

DIAGNOSIS (Figs 95, 96). Marine. About 20–44 × 16–23 (usually less than 20) µm. Shape of prepared individuals egg-like, circular in cross section (Fig. 95). Macronucleus spherical, central. Micronucleus not observed. Cytoproct an elongated (approximately 8 µm) slit near posterior pole, lying in the same latitude as cytostome and suture at ends of ciliary spirals. Contractile vacuole pore not observed. Except for elongated caudal cilium, all somatic cilia restricted to anterior half of cell, arranged in at least four spirals (a few individuals possess a partial or even complete fifth spiral, and even a few cilia of a sixth spiral). Outer vestibular kinety in a semicircle dipping posteriorly into vestibulum and terminating near cytostome. Inner vestibular kinety with three regions: (1) anteriormost two isolated tufts of approximately five cilia each, (2) a row of kinetosomes closely paralleling the outer kinety, extending from the tufts down to cytostome, (3) posteriormost a J-shaped field of cilia. As already mentioned, this interpretation of the oral structure is a little erroneous and incomplete.

OCCURRENCE AND ECOLOGY. Like the other species of this genus *T. pleurispiralis* is bacterivorous and occurred only irregularly in New Hampshire tidal salt marshes (Borror, 1972).

REMARKS. This species differs from the other members of the genus in number and location of ciliary spirals, which are restricted to the anterior half of body. Unfortunately, Borror (1972) did not give a drawing from life. Thus, the real body shape is unknown. Redescription is needed.

Genus ***TROCHILIOPSIS*** Penard, 1922

DIAGNOSIS. Microthoracidae Wrześniowski, 1870 with cytostome in the anterior third of body. Three preoral kineties subapically on the left body side. Somatic kineties from either side terminate near the pointed beak-like region formed by the oral structures. Apex smooth. Rightmost somatic kinety of the right side interrupted. Contractile vacuole located almost centrally. Freshwater, polysaprobic.

TYPE-SPECIES. *Trochiliopsis opaca* Penard, 1922.

REMARKS. *Trochiliopsis* shows many characters which are very likely homologous to genera of the family Microthoracidae Wrześniowski 1870 according to the classification of Foissner (1985*b*). Thus, a separation of *Trochiliopsis* at the familial level as suggested by Jankowski (1975) is not justified (Compare Corliss, 1979; Curds, 1982). On the contrary, the organization of *Trochiliopsis,* especially the general appearance of the infraciliature and the location and structure of the oral apparatus, allows a classification close to the genus *Stammeridium.* These similarities might have induced Kahl (1931) to synonymize *Trochiliopsis* with *Trichopelma* Levander and *Leptopharynx* Mermod. There are just sufficient differences in the location of the preoral kineties, the paroral membrane, and the shape of the anteriormost region for separating these two genera. Furthermore, by a trivial twist of some organelles of *Trochiliopsis,* the typical organization of the genus *Stammeridium* can be achieved (Figs 126, 127): The preoral kineties move to the apex between serrated processes, the paroral membrane gets located obliquely to the longitudinal axis and the contractile vacuole moves close to the ventral side.

Key to the genera of Microthoracina Jankowski 1967 (based on Foissner 1985*b*)

1a	Microthoracina with somatic cirri-like organelles, fusiform extrusomes, and wide-meshed silverline system	(Discotrichidae) ***Discotricha***
1b	Microthoracina with normal cilia, anchor-like extrusomes, and granular or fine-meshed silverline system	2
2a	Microthoracina with more than 10 uninterrupted somatic kineties	(Pseudomicrothoracidae) ***Pseudomicrothorax***
2b	Microthoracina with fewer than 10, usually 6 partly interrupted somatic and three preoral kineties (Microthoracidae)	3
3a	Oral apparatus ventrally in the posterior third of body	***Microthorax***
3b	Other	4
4a	Oral apparatus ventrally between middle and posterior third of body, body more or less oblong	***Drepanomonas***
4b	Other	5
5a	Oral apparatus between middle and anterior third of body, rightmost somatic kinety or right side uninterrupted, preoral kineties run in distinct furrows from the ventral to the right body side and form a keel	***Leptopharynx***
5b	Other	6
6a	Rightmost somatic kinety of right side interrupted, preoral kineties run anterior-posteriorly on the left side of the body, paroral membrane *circa* half body length	***Trochiliopsis*** single species: ***Trochiliopsis opaca***
6b	Preoral kineties apically in furrows, apex distinctly serrated, paroral membrane shorter than a third of body running obliquely to the longitudinal axis	***Stammeridium*** single species: ***Stammeridium kahli***

Description of species

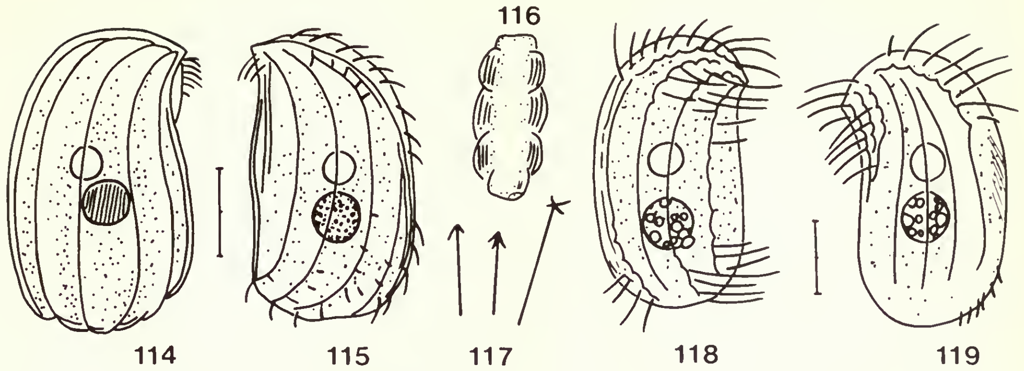
Trochiliopsis opaca Penard, 1922

Trichopelma opaca Kahl, 1931
Leptopharynx opaca Detcheva, 1972

NEOTYPE-SPECIMENS. Slides (protargol silver impregnated and dry silvered) of neotype-specimens have been deposited in the British Museum (Natural History) in London, reference numbers 1986:5:30:4–5.

REDESCRIPTION (Figs 114–131, Table 3). Type species of the genus. Freshwater. *In vivo circa* 30–40(–50) × 17–20 µm. Body outline oval, anteriorly curved slightly to the ventral side terminating in a pointed beak-like region (peak). Body strongly compressed laterally (*circa* 2 : 1). Somatic kineties in deep, crenelated furrows, which terminate near the oral peak. Macronucleus spherical, more or less centrally located, *in vivo* hardly discernible. Micronucleus closely attached to the macronucleus. Contractile vacuole centrally located, close to the right lateral surface, diameter about 4 µm; contractile vacuole pore at the end of the paroral membrane. Cytoproct slightly posterior to the contractile vacuole pore, visible as black line in dry silvered specimen (Fig. 130). Pellicle rigid, colourless, opaque. Extrusomes about 3 µm, fusiform, scattered over the whole body in the ribs between the furrows, show four anchor-like processes at the distal end in the exploded phase. Probably feeds on bacteria, but no food vacuoles were found. Slow, trembling and swaying movements.

Length of cilia 8–10 µm. Six somatic kineties (K1–6), three preoral kineties (P1–3), and a short x-kinety (Figs 124, 125). K1 anterior with 8–10, posterior with 4, K2 anterior with 2, posterior with 5–6, K3 anterior with 12–16, posterior with 5–8, K4 (anterior) with 6–8, K5 anterior with 3–4, posterior with 2, K6 with 10–12 kinetosomes. At the end of K4 and in the middle of K5 sometimes a single unciliated kinetosome, respectively. Basal bodies of K1–5 mostly paired, K6 always with single kinetosomes. Preoral kinety 1 with 4–5 pairs, preoral kinety 2 constantly with 5 singles, and preoral kinety 3 constantly with 7 singles. x-kinety with 1–2 paired basal bodies located left of the posterior end of the paroral membrane (Figs 120–126).


116
114
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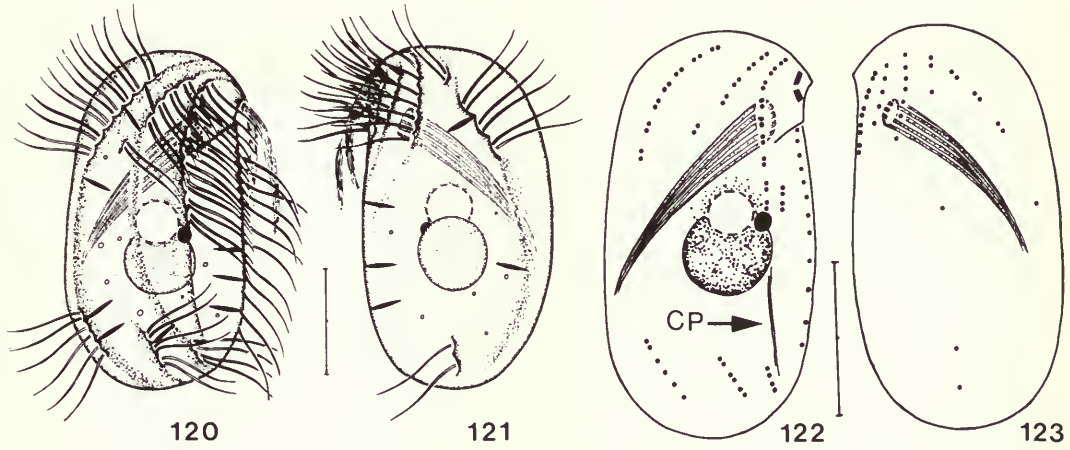
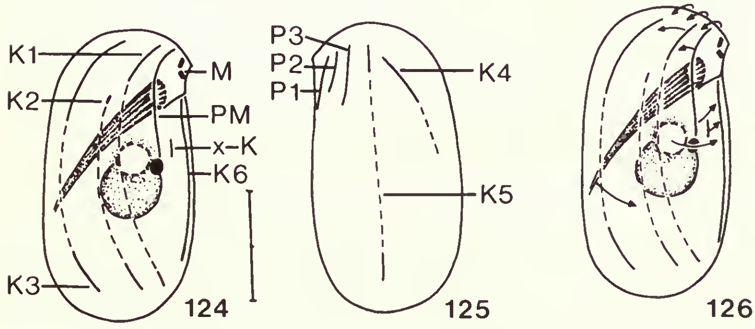
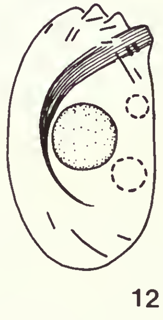
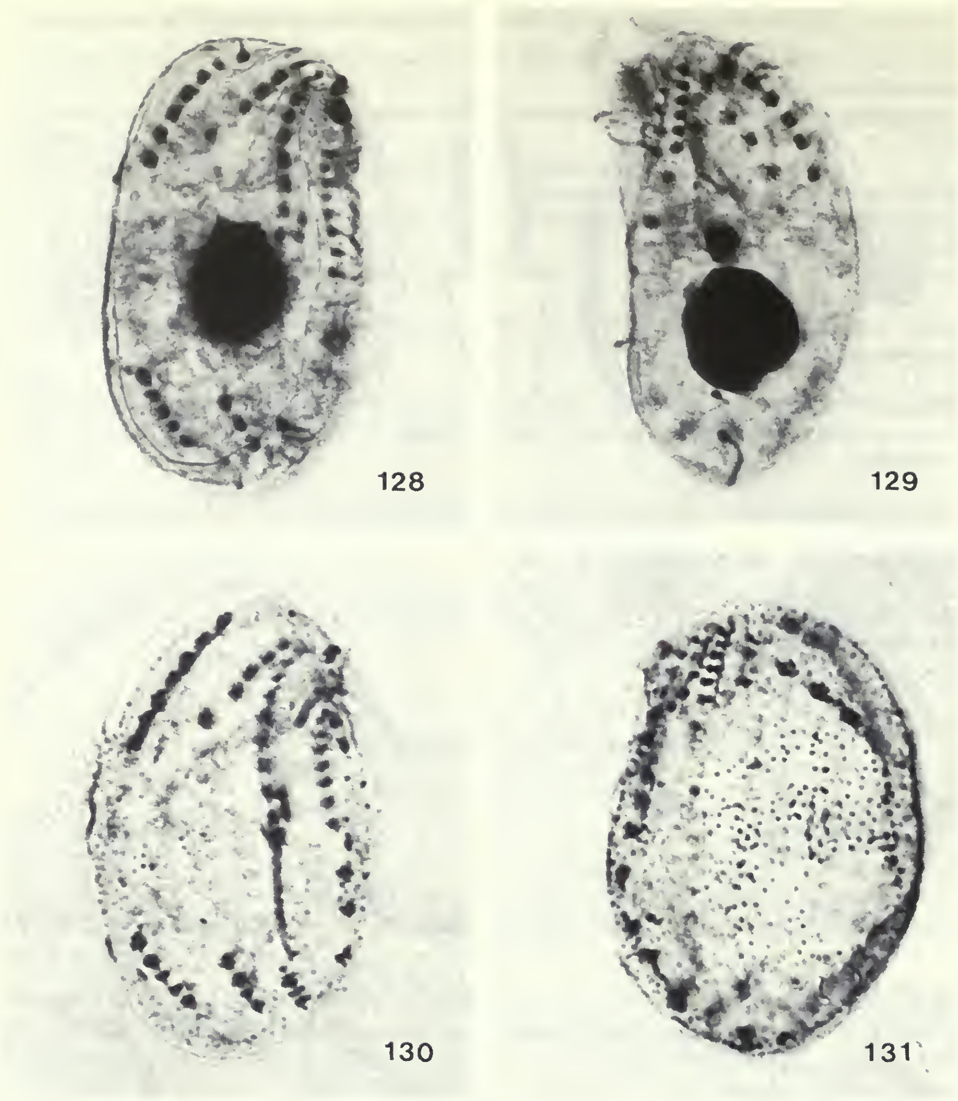

CP
120
121
122
123


K1
K2
K3
M
PM
x–K
K6
P3
P2
P1
K4
K5
124
125
126



Figs 114–126 *Trochiliopsis opaca*, scale = 10 μm each. **114–117** After Penard (1922). **114, 115** Right and left lateral view. **116** View from the apex. **117** Extrusomes with 2, 3, and 4 processes. **118, 119** After Kahl (1931), right and left side. **120–123** Originals, from life and protargol silver stained specimens, right and left side respectively. CP, cytoproct. **124, 125** Schematized organization of *T. opaca*, right and left lateral view. K1–6, somatic kineties 1–6; M, adoral membranelles; PM, paroral membrane; P1–3, preoral kineties 1–3; x–K, x-kinety **126** Probable evolution of *Stammeridium* from *Trochiliopsis*.

Fig. 127 Schematic organization of the genus *Stammeridium* (after Foissner, 1985*b*).



Figs 128–131 *Trochiliopsis opaca.* **128, 129** Protargol silver impregnated specimens, right and left side. **130, 131** Dry silver impregnated specimens, right and left side.

Probably only two adoral membranelles, located at the oral peak. Anterior adoral membranelle most likely built up by two rows, posterior one probably by three rows of kinetosomes. Paroral membrane with 8–9 paired basal bodies (Figs 120, 122, 124). Cyrtos invisible in life even with interference contrast, but slightly impregnated with protargol silver.

Silverline system granular or very fine-meshed.

OCCURRENCE AND ECOLOGY. Penard (1922) found few individuals between dead leaves of the 'swan pond' at Ariana ('. . . à l'étang des Cygnes', Switzerland). Kahl (1931) noted *T. opaca* sporadically in the sapropel and sometimes numerously in sapropelic infusions of *Glyceria.* Lackey (1938) recorded it once from a polluted stream, twice from a trickling filter, and five times from an activated-sludge chamber. Noland & Gojdics (1967) mentioned that *T. opaca* occurs when the sludge has reached the finely particulate stage and the bacteria in it are well distributed. Detcheva

(1972) listed some Bulgarian habitats, namely a pond in the surroundings of the village Bosnek in the Witoscha mountains, a marshy meadow in the vicinity of the village Kasitschene near Sofia, and a river in the Wrâbniza quarter of Sofia. Apart from in activated sludge, we found this species once in the polysaprobic zone of a heavily polluted river (Ager near Lenzing, Upper Austria). These localities suggest *T. opaca* to be a good indicator of heavily polluted (polysaprobic) conditions. It might also have some tolerance of H_2S.

Table 3 Biometrical characterization of *Trochiliopsis opaca*

Character[1]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	25·66	26·0	1·12	0·37	4·4	24·0	27·0	9
Body, width	13·22	13·0	0·83	0·28	6·3	12·0	15·0	9
Macronucleus, length	6·33	6·5	0·35	0·12	5·6	6·0	7·0	9
Macronucleus, width	6·11	6·0	0·42	0·14	6·8	5·5	7·0	9
Distance from apex to the beginning of macronucleus	12·22	12·0	1·30	0·44	10·6	10·0	14·0	9
Micronucleus, length	1·62	1·6	0·30	0·10	18·7	1·2	2·0	9
Micronucleus, width	1·51	1·5	0·31	0·10	20·8	1·0	1·8	9
Number of kinetosomes of paroral membrane	17·78	18·0	0·67	0·22	3·7	16·0	18·0	9
Number of kinetosomes of anterior kinety 1	8·22	8·0	0·67	0·22	8·1	8·0	10·0	9
Number of kinetosomes of posterior kinety 1	4·00	4·0	0·00	0·00	0·0	4·0	4·0	9
Number of kinetosomes of anterior kinety 2	2·00	2·0	0·00	0·00	0·0	2·0	2·0	9
Number of kinetosomes of posterior kinety 2	5·89	6·0	0·33	0·11	5·7	5·0	6·0	9
Number of kinetosomes of anterior kinety 3	13·11	12·0	1·45	0·48	11·1	12·0	16·0	9
Number of kinetosomes of posterior kinety 3	6·11	6·0	0·93	0·31	15·2	5·0	8·0	9
Number of kinetosomes of kinety 4	6·67	6·0	0·87	0·29	13·0	6·0	8·0	9
Number of kinetosomes of anterior kinety 5	3·11	3·0	0·33	0·11	10·7	3·0	4·0	9
Number of kinetosomes of posterior kinety 5	2·00	2·0	0·00	0·00	0·0	2·0	2·0	9
Number of kinetosomes of kinety 6	10·33	10·0	0·71	0·24	6·8	10·0	12·0	9
Number of kinetosomes of the x-kinety	3·78	4·0	0·67	0·22	17·6	2·0	4·0	9
Number of kinetosomes of preoral kinety 1	9·89	10·0	0·33	0·11	3·4	9·0	10·0	9
Number of kinetosomes of preoral kinety 2	5·00	5·0	0·00	0·00	0·0	5·0	5·0	9
Number of kinetosomes of preoral kinety 3	7·00	7·0	0·00	0·00	0·0	7·0	7·0	9

[1] See footnote Table 1

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British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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J. E. Hill & D. L. Harrison

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PRESENTED

The baculum in the Vespertilioninae (Chiroptera: Vespertilionidae) with a systematic review, a synopsis of *Pipistrellus* and *Eptesicus*, and the descriptions of a new genus and subgenus

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Synopsis

Current classification of the Vespertilioninae rests chiefly on a suite of mainly adaptive characters, among which facial shortening throughout the subfamily with consequent changes in the structure, size, relative position and number of the incisive and premolar teeth features prominently. Such characters may not necessarily reflect relationships or phyletic diversity, and sometimes do not serve properly to distinguish the genera that they purport to define, as in the distinction of *Pipistrellus* and *Eptesicus*, where generic boundaries remain unclear. The search for possibly less strongly adaptive features suggested the possibility that the morphology of the os penis or baculum might prove valuable in the study of the systematics of these genera and perhaps in the subfamily as a whole.

This paper reviews earlier studies of the baculum in the Chiroptera and their relevance to systematics in the Order, with an examination of its gross morphology throughout the Vespertilioninae, especial attention being given to species currently allocated either to *Pipistrellus* or to *Eptesicus*. A synoptic review of the species

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content of these genera is presented, with the recognition and definition of subgenera and included species groups: three such (*pumilus, capensis* and *tenuipinnis*) currently referred to *Eptesicus* on dental grounds seem instead more closely related to *Pipistrellus* to which they are here transferred. One subgenus of *Pipistrellus* is described as new (p. 250).

The Vespertilioninae as a whole display a wide range of bacular variation, which falls into two major and several minor groups. This has suggested a revision of the current classification of the subfamily, combining bacular features with those conventionally in use. Bacular morphology provides a clear indication that the 'Nycticeini' (or 'Nycticeiini') is an artificial grouping and that the genus *Nycticeius* as presently understood is composite. Currently it is held to include two species, the North American *humeralis* and the African *schlieffenii*: these are here thought to be sufficiently characterised to justify generic separation and a new generic name is proposed for *schlieffenii* (p. 254).

A suggested classification of the subfamily is presented, with a tabulated review of earlier classifications; possible relationships between the constituent genera are discussed and the zoogeography of the bacular types within the subfamily is examined.

Introduction

A penial bone is known to occur among mammalian Orders in the Insectivora, Chiroptera, Primates, Rodentia and Carnivora. Variously called the os penis, os priapi or os glandis, it was first named the baculum by Thomas (1915*a*), the corresponding structure in the female, the os clitoridis, being later called the baubellum by Shortridge (1934: 327, footnote). The features of the baculum have been used extensively in attempts to determine phyletic relationships at various systematic levels (Patterson & Thaeler, 1982). Thomas (loc. cit.), for example, suggested that the baculum might provide evidence valuable in the subfamilial classification of the Sciuridae and indeed pointed out that in this connection there were no bacular features to support the association of the dwarf squirrels in a separate subfamily, the Nannosciurinae. More commonly, bacular features have been used to indicate or determine relationships within genera in the Sciuridae, among New World rodents, and in the Mustelidae. Such characteristics have been employed in species descriptions, especially where bacular variation is pronounced, and also for age determination. Numerous examples of these uses of the baculum are summarised by Patterson & Thaeler (loc. cit.) while Burt (1960) gave an account of the earlier of such studies. Similar early accounts of the baculum in the Chiroptera are reviewed by Hamilton (1949).

The presence of a baculum in some at least of the Chiroptera has been long established. Daubenton (1760) described and illustrated (in part) the baculum of *Nyctalus noctula* and Blainville (1840) similarly studied the baculum of *Rhinolophus ferrumequinum, R. hipposideros, Vespertilio murinus* and again of *Nyctalus noctula,* the latter author providing perhaps the first accurate and quite detailed drawings of this structure. Later workers such as Ercolani (1868), Robin (1881), Gilbert (1892), Rauther (1903), Gerhardt (1905) and Chaine (1926) provided further details of penial and bacular morphology in the Chiroptera, Chaine in particular discussing and illustrating the baculum in several species and to some extent summarising earlier work in the field. However, none attempted to use the structure of the baculum for systematic purposes.

The first use of the baculum in chiropteran systematics appears to be by Thomas (1915*b*) who employed bacular characteristics in defining the species of *Nyctophilus.* This worker clearly foresaw the value of bacular features in the definition of some at least of the species of bats, beginning from that time a collection of vespertilionid bacula at the British Museum (Natural History) although subsequently making little use of the material that was accumulating, except in 1928 employing bacular characters to separate Indo-Chinese species of *Pipistrellus* (Thomas, 1928*a, b*). Since then the baculum has been utilised in a variety of taxonomic studies of bats, for example by Krutzsch (1959, 1962) and Lanza (1969) to examine its value in indicating relationships in the Megachiroptera, by Topál (1970*a*) in determining the affinities of *Ia,* or by Heller & Volleth (1984) as an indicator of relationship among the species of *Pipistrellus* and *Eptesicus.* The baculum of *Plecotus* was found valuable by Lanza (1960) in discriminating between *P. auritus* and *P. wardi* (= *P. austriacus*): the subsequent use of the baculum in distinguishing these species is summarised by Corbet (1964). Genoways & Jones (1969) found that bacular features distinguished closely related species of North American *Myotis*, LaVal (1973*a*) employing bacular characters for the same purpose among the Neotropical species of this genus.

The emphasis placed on bacular characters in chiropteran systematics is perhaps best illustrated by the number of studies devoted chiefly to bacular structure, often on a regional or faunal basis, as for instance the work by Hamilton (1949) and Krutzsch & Vaughan (1955) on North American species, by Brown *et al.* (1971) on Neotropical bats, by Topál (1958) on central European species, by Bhatnagar (1967), Agrawal & Sinha (1973), Sinha (1976) and Khajuria (1979, 1980, 1982) on Indian bats, or by Wassif & Madkour (1972) and Wassif, Madkour & Soliman (1984) on Egyptian bats. Bacula are sometimes studied in discrete taxonomic groupings, as for example those of New World molossids by Brown (1967) or of Malaysian *Hipposideros* by Zubaid & Davison (in press). Thus among the Chiroptera the baculum has been employed as a source of taxonomic features at several systematic levels, but primarily to indicate degrees of relationship or for separation at the specific and sometimes the generic grades, or especially for distinguishing closely related, often sympatric species whose conventional morphological characters are otherwise very similar, as in *Myotis* and *Plecotus*.

Functional and systematic significance of the baculum

Conflicting hypotheses for bacular variation were reviewed in detail by Patterson & Thaeler (1982). These authors proposed that among rodents at least the probability was that the baculum has a precise reproductive purpose and functions primarily as a device contributing to species isolation. Bacular differences among closely related taxa might well then take an exaggerated form. As such, the baculum would be therefore a poor basis for supra-specific classification, but an excellent structure for species diagnosis. Thus they would not consider a phyletic basis for bacular variation to be appropriate. They admit, however, that while in some rodent groups there are patterns of bacular morphology that do not agree with phyletic divergence as indicated by other morphological features, there exist also gross patterns of bacular variation in other groups that do in fact conform with accepted phyletic relationships. Indeed, they remarked that there can be little doubt that the baculum exhibits phyletic weight and consequently may serve as a valuable taxonomic tool. Moreover, taxa that differ in external and cranial characters may have similar bacula, while others that are similar in such features may exhibit highly distinctive genitalia. Patterson & Thaeler (loc. cit.) suggested that although bacular morphology reflects phyletic history on a gross scale, discordance between patterns of bacular and phyletic divergence supports a functional interpretation of bacular variation, especially at the species level.

Similarly, opinions vary as to the value of bacular morphology in chiropteran systematics. Hamilton (1949) examined the baculum in North American vespertilionids and concluded that in this family the baculum was useful in defining relationships when considered with skull and other skeletal characteristics. Thus he was able to suggest that the close similarity between the bacula of *Myotis* (Fig. 19i, j) and *Pizonyx* (Fig. 19k) indicated their close relationship, and that the dissimilarity between the bacula of *Pipistrellus subflavus* (Fig. 2d) and *P. hesperus* (Fig. 8d) suggested generic or at least subgeneric difference. This author also noted that in most instances among North American vespertilionids there were marked generic differences in the baculum. He considered that further study was needed to determine the usefulness of the baculum in chiropteran systematics and that with time and sufficient material the bone might be utilised in classification. These conclusions were reinforced by Krutzsch & Vaughan (1955) who examined the bacula of further North American species. They remarked that in the case of those that are closely related the baculum can serve as a criterion in judging relationship when other clear cut distinguishing characters are lacking. These authors found bacular variation in closely related bat species to be chiefly in shape, detail of outline, and gross size: their study led to the belief that in at least some superficially similar species well marked and consistent bacular differences reinforced the more subtle external and cranial dissimilarities.

Krutzsch (1959) accepted the view that the baculum can provide additional evidence for classification, or, in the absence of other clearly defined characters, can serve as a criterion in judging relationship. He added in relation to the Pteropodidae that by virtue of its relative simplicity and structural stability the baculum might well serve to help place entities of doubtful relationship in their natural position, although they might be otherwise morphologically contradictory. Among pteropodids he found that infrageneric differences in the baculum involved minor details of shape, outline and size. Genera, however, might be separated by more profound differences. His study suggested that although within the genus well marked and consistent differences existed between the bacula of individual species, there was nevertheless a basic similarity in pattern throughout the genus, leading to the suggestion that marked variants from this morphological standard in a single genus might provide grounds for a reappraisal of the affinities of the variant. A further study (Krutzsch, 1962) confirmed these opinions, especially in the broad agreement of bacular variation in pteropodids with the taxonomic arrangement of this family by Andersen (1912) and by Tate (1942*b*). Krutzsch concluded that strong intrageneric similarities exist among the bacula of pteropodids, but that representative bacula of different genera differ distinctly: although serving well as a source of diagnostic features for the genus, the baculum does not seem to offer exceptional insight into suprageneric relationships. The large genus *Pteropus*, however, to some extent proves to be an exception, with various of its many species demonstrating considerable variation in bacular structure: on occasion differences between species equal those between some megachiropteran genera.

Lanza (1969) examined the baculum of *Pteropus* in detail and found that its bacular morphology did not conform to the classification proposed by Andersen (1912), a conclusion also reached by Davis (1947) who examined only five species. Lanza found that in many cases bacula of an identical size and shape could be found among species belonging to the same group as well as to different groups; or that the baculum could be extremely different among forms apparently otherwise very closely related. Thus in this genus he found the baculum to be of limited value in phyletic analysis. Similarly, LaVal (1973*b*) found that with one exception the bacula of the various species of the vespertilionid *Rhogeessa* are not sharply differentiated from each other: although in shape they show substantial geographic and individual variation within species they seem nevertheless to differ between species in areas of sympatry or near sympatry. Harrison & Brownlow (1978) found that individual variation in the baculum of adults of another vespertilionid, *Scotophilus*, was such that it rendered this structure of little or no value in species diagnosis in this difficult genus.

Martin (1978) discussed the adaptive value of the baculum in bats, having found a wider range of structural variation among several pteropodid species than was previously thought. He considered that the baculum may have a number of roles of varying adaptive significance in supporting the penis, as a stimulatory structure, or in preventing urethral closure during the pressures of copulation. Although these might allow the baculum to maintain morphological stability within certain taxonomic units, this possible variability of function he thought tended to reduce its value in classification at the specific and subspecific levels.

Despite these possible limitations, many authors admit at least the species-specificity of bacular variation among bats, using the baculum to provide additional characters to separate species that sometimes otherwise closely resemble each other. Some examples have been mentioned: others include Wallin (1969) who drew attention to bacular differences in Japanese *Pipistrellus* and who used such differences to define two species groups in *Vespertilio*, or Baagøe (1973) who utilised bacular characters in comparing sibling species of European *Myotis*. Zubaid & Davison (in press) found the baculum to be specifically diagnostic among Malaysian *Hipposideros*. In some genera authors have routinely described and illustrated the baculum of new species: for instance Sinha (1969) in describing *Pipistrellus peguensis* compared its baculum with the bacula of the related species. Similarly, McKean *et al.* (1978) described and illustrated the baculum of *'Eptesicus' sagittula*, comparing it with the bacula of other Australian *'Eptesicus'*, while Kitchener (1976) employed the baculum of *'Eptesicus' douglasorum* in the same way. Bacular characters sometimes form an essential part of revisionary study, as by Kitchener *et al.* (1986) in defining and keying the Australo–Papuan representatives of *Pipistrellus* and *Falsistrellus*. The baculum has also featured in generic revision, Hill (1966*a*) for example describing and illustrating that of *Philetor* in the course of such a study, or (1976) that of the majority of the species of *Hesperoptenus*.

Bacular variation has also been employed for generic and subgeneric distinction within the

Vespertilioninae. Wallin (1969) used penial characters in establishing *Vespertilio* as a genus distinct from *Eptesicus* and in recognising *Hypsugo* as a subgenus within *Pipistrellus,* while Topál (1970*a*) noted that bacular morphology allied the aberrant genus *Ia* more closely to *Eptesicus* than to *Pipistrellus* with which it had been associated by some authors. Heller & Volleth (1984) summarised published illustrations of the bacula of *Pipistrellus, Eptesicus* and some of their associated genera, drawing attention to their taxonomic implications. At a further systematic level, Pine *et al.* (1971) discussed the penial and bacular morphology of *Antrozous* and *Bauerus* in relation to the presumed affinities of these North American genera to the Australian and New Guinea genera *Nyctophilus* and *Pharotis* with which they have been associated in the subfamily Nyctophilinae.

It is clear from the foregoing account that the baculum is regarded as a valuable source of diagnostic information by many students of chiropteran systematics. This seems especially true in the Vespertilioninae, a subfamily in which diagnosis and definition at both specific and generic levels is sometimes difficult if only the orthodox morphological characters of external, cranial and dental structure are to be relied upon.

Nature and scope of this study

The basis of the current classification of the Vespertilioninae was first set out in detail by Miller (1907), who recognised a total of thirty-two genera in the group, with diagnoses and short descriptive accounts. The classification of Miller was based chiefly on external, cranial and dental features. Tate (1942*a*) reviewed the characters used for diagnosis in some detail, dividing the subfamily into four main (tribal) aggregations, and attempting to quantify the interrelationships of its many genera. The major outlines of his classification have since been followed, sometimes with local modification as for instance by Koopman (1984*a, b,* 1985) who subsumed the subfamily Nyctophilinae into the Vespertilioninae. Hill (1966) pointed out that the subfamily comprises a complex of closely interrelated genera separated in some instances by comparatively slender or even rather arbitrary distinctions, the patterns of relationship often obscured by parallelism or convergence.

The narrowness of the orthodox distinctions that define many of the constituent genera of the Vespertilioninae has led to much taxonomic combination and recombination since Tate wrote. This situation is exemplified by the more extreme variants of classification that have been proposed. For example, Kuzyakin (1944, 1950, 1965) included *Pipistrellus* and *Eptesicus* in *Vespertilio* while Simpson (1945) included *Glischropus, Scotozous, Nyctalus* and *Ia* in *Pipistrellus* and *Rhinopterus, Hesperoptenus, Tylonycteris, Mimetillus, Philetor, Histiotus* and *Laephotis* in *Eptesicus.* A yet more extreme viewpoint was adopted by Sokolov (1973) who considered that *Vespertilio* should include not only *Pipistrellus* and *Eptesicus* as was thought by Kuzyakin, but also all of the other above mentioned genera except *Nyctalus.* Horáček & Hanák (1985*a, b*) commented that the concepts of Kuzyakin and Sokolov (with the inclusion of *Nyctalus*) might be provisionally accepted, at least until factual proof of paraphylly in the group was forthcoming. Nevertheless, they considered this to be a retrograde solution since it expresses nothing of the factual diversity of the group, proposing instead that the problematic taxa should be arranged in separate genera, their diagnoses then making their content clearer though narrower. Both Simpson and Sokolov also included *Scotoecus* and *Scotomanes* in *Nycticeius* as then understood, *Baeodon* in *Rhogeessa, Glauconycteris* in *Chalinolobus* and *Dasypterus* in *Lasiurus* to produce a heavily 'lumped' classification. The status of some such as *Scotoecus, Dasypterus* and *Idionycteris* has varied from one author to another for decades: in the Australian region *Scoteanax* and *Scotorepens* have recently achieved generic rank after many years as nominal subgenera (Kitchener & Caputi, 1985) while *Ia* has once again reverted to *Pipistrellus* (Koopman 1984*a, b,* 1985) after a brief spell with *Eptesicus.* The major variants of vespertilionine classification are summarised in Table 1.

Many of the characters used to define taxa and relationships among the Vespertilioninae appear strongly adaptive and of equivocal value in generic and suprageneric systematics. Most concern ear size and shape, tragal structure, the architecture of the skull, and the number and formation of the teeth. Zima & Horáček (1985) pointed out that the use of the morphological characters employed hitherto in the classification of the Vespertilionidae as a whole might not lead invariably to correct taxonomic conclusions, their degree of differentiation perhaps reflecting the orientation and intensity of selection pressure rather than actual phyletic relationships. These authors indicated an urgent need for new, sufficiently reliable and taxonomically useful criteria based on features that did not possess a direct adaptive significance, including among these the morphology of the reproductive organs and the baculum.

Much weight has been placed in the past upon the progressive shortening of the muzzle apparent throughout the Vespertilioninae with concomitant reduction and loss of the incisors and premolars (Tate, 1942*a*). In the incisive dentition the first upper tooth (i^1)[a] is absent, as in all bats. Reduction results in the remaining inner tooth (i^2) becoming peg-like and unicuspid, although sometimes quite massive, in a reduction in size of the outer tooth (i^3), its displacement inwards or outwards, or in its eventual obsolescence or loss. In the mandible, the first (i_1) and second (i_2) incisor teeth are invariably present, but exceptionally the third (i_3) may be absent. The process also involves the reduction and loss of the second upper and lower premolars ($pm\frac{3}{3}$) and then of the anterior upper premolar (pm^2): thus the premolar formula ranges from pm $\frac{-}{-}\frac{2}{2}\frac{3}{3}\frac{4}{4}$ to pm $\frac{-}{-}\frac{-}{2}\frac{-}{-}\frac{4}{4}$ the first upper and lower premolars ($pm\frac{1}{1}$) being presumed to be those that are absent from all bats. Seven different combinations of incisors and premolars occur in the subfamily, if *Antrozous* and *Bauerus* are included. The full complement is usually taken as the primitive condition, the reduction and disappearance of teeth as derived. These are summarised in Table 2, which gives the incisive and premolar formulae usually attributed to each of the various genera. However, *Myotis* occur in which pm^3 or $pm\frac{3}{3}$ are absent (Hill & Topál, 1973), thus in the first instance producing the formula typified by *Lasionycteris* or *Plecotus*, in the second the formula for *Pipistrellus* or *Nyctalus*; pm^2 may be absent from *Pipistrellus* to give the arrangement for *Eptesicus*, or may be present in *Eptesicus* to produce the formula for *Pipistrellus* (Hill & Topál, loc. cit.); i^3 is variable in *Scotozous* (of 45 examined, present in 34, absent from one side or the other in 8, completely absent from 3), when totally absent to produce the incisive formula that usually characterises *Nycticeius* and its associates (but Thomas & Wroughton (1908) report an example of *'Nycticeius' schlieffenii* in which the left i^3 is present); pm^2 is variable in *Scotoecus* (Hill, 1974) and in *Chalinolobus* (Ryan, 1966; Koopman, 1971), and very rarely may be present in *'Nycticeius' schlieffenii* (Dobson, 1878; Thomas, 1890).

Most genera of Vespertilioninae can be defined by other features besides those of the incisive and premolar dentition, although sometimes only in differing combinations. Thus although some species exist that combine the external features of *Myotis* with the dental formula of *Pipistrellus* to the extent that initially they (*annectans, ridleyi*) were described in the latter genus, other characters such as the form and structure of the tragus and the structure of the incisors enable them to be referred confidently to *Myotis* (Topál, 1970*b*; Hill & Topál, 1973). Another (*rosseti*) was first described in *Glischropus*, subsequently removed to *Pipistrellus* by Hill (1969) and finally (with *ridleyi*) to *Myotis* by Hill & Topál (loc. cit.). However, the genera *Pipistrellus* and *Eptesicus* do not offer further conventional characters in this way and are separated for the most part by the presence of pm^2 in the former and its absence in the latter. Wallin (1969) and Hill & Topál (loc. cit.) discussed the variability of this tooth in *Pipistrellus* and *Eptesicus* in detail, the latter authors concluding that the presence or absence of pm^2 can have no universal validity in defining the two genera. Heller & Volleth (1984) also examined the relevance of pm^2 in separating *Pipistrellus* and *Eptesicus* and concluded that it does not seem to be a reliable characteristic, a classification based on it perhaps misrepresenting true relationship. Tate (1942*a*) recognised this difficulty but adhered to the conventional practice of separating the two genera by this feature, and indeed the majority of authors have retained the distinction as a matter of convenience, often using the extent of reduction and degree of displacement of $pm\frac{2}{2}$ from the line of the toothrow as a diagnostic feature between the species of *Pipistrellus*.

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[a] Dental notation of Miller (1907)

Koopman (1975) has commented upon this problem. This author examined African species allocated variously to *Pipistrellus* and *Eptesicus* in an attempt to find some other character that would divide this large assemblage into two major groups. He could find none among the usual suite of morphological features. Although he found no African *Pipistrellus* species that closely resembled the *hottentotus, tenuipinnis* or *floweri* groups of *Eptesicus* and no African member of the latter genus that was similar to the *pipistrellus, hesperus, savii* or *rueppellii* groups of *Pipistrellus* as he defined them, he did find a resemblance amounting in some cases to virtual identity (if pm^2 was ignored) between the *kuhlii* group of *Pipistrellus* and the *Eptesicus capensis* group. Expanding a view first expressed by Tate (1942*a*) in his account of *Eptesicus,* Koopman commented that it is probable that the anterior upper premolar has been lost more than once here, and that true phyletic relationships run across the 'generic' line. He thought that it is even possible that in some cases a '*Pipistrellus* species' and an '*Eptesicus* species' are actually conspecific, but was of the opinion that the available material was insufficient to establish this with certainty for any such pair at the present time. Although retaining *Pipistrellus* and *Eptesicus* as separate genera since he believed that the problem should be attacked on a cosmopolitan basis, he remarked that such an arrangement is almost certainly wrong. More recently, Horáček & Hanák (1985–1986) have offered further definitions of *Pipistrellus, Hypsugo* and *Eptesicus.*

Many varying interpretations can be placed upon external, cranial and dental morphology or on karyological data in the Vespertilioninae. These range from the relationship of one species to another to suprageneric relationships, even to the view that *Pipistrellus* and *Eptesicus* may be polyphyletic. Menu (1984), for example, remarked that an exhaustive odontological study of the Vespertilioninae indicated that *Pipistrellus* includes species wrongly associated by reason of their identical dental formula, but which are not related. Williams & Mares (1978) discussed the karyology of *Eptesicus,* which as currently defined they thought seemed to be a composite taxon, encompassing perhaps several phyletic lines of pipistrelloid species with reduced numbers of premolars. Heller & Volleth (1984) suggested that *Pipistrellus* may be a very heterogeneous assemblage and after reviewing the relevance of pm^2 in separating this genus from *Eptesicus* considered the baculum to be a more reliable guide to the phylogeny of the species of *Pipistrellus* and *Eptesicus,* using its features to supplement their findings from karyological data. Many years before this Tate (1942*a*) remarked that it seemed probable that study of the baculum in the Microchiroptera would yield valuable results, with the implication that this might have significance in the classification of the Vespertilionidae. Indeed, Tate records that G. M. Allen had gathered together a number of bacula representing many of the species of *Pipistrellus* which he intended to employ in revising the genus. Moreover, relatively few species of the nominal genera *Pipistrellus* and *Eptesicus* have so far been studied: the impression gained from the literature is that *Pipistrellus* as currently understood is dignified chiefly by a long, slender shafted baculum and most *Eptesicus* as it is presently classified by a small, triangular structure, which we have found not to be the case.

Initially our intention was to examine the bacula of as many species of *Pipistrellus* as possible to establish the pattern of bacular variation within the genus, and to compare it with the species groupings proposed by Tate (1942*a*) and by Koopman (1973, 1975). As the work progressed, however, it became increasingly apparent that its implications extended far beyond the limits of this nominal genus and that it was necessary in addition to study the bacula of *Eptesicus* so far as we were able, and to examine the boundary between these two conventional groupings. Finally, to place our findings in proper perspective, we have surveyed the bacula of most of the remaining genera of the Vespertilioninae and have attempted to assess the generic significance of bacular variation in the subfamily. We have also examined the bacula of *Nyctophilus* and *Pharotis,* both usually referred to the closely related subfamily Nyctophilinae. This has been united recently with the Vespertilioninae (Koopman, 1984*a, b,* 1985) and is thus relevant to our study.

We have made no detailed examination of the gross morphology of the chiropteran penis except insofar as it is reflected by bacular structures. Nor have we attempted to study its histomorphology. These features are discussed by Smith & Madkour (1980) in an effort to elucidate their relevance to interordinal and infraordinal phylogenetic relationships, and who review earlier studies of penial morphology.

Materials and methods

We have been able to examine bacula from the majority of species currently listed in *Pipistrellus* and from most of those presently assigned to *Eptesicus*. In a few instances we have relied upon illustrations and descriptions from the literature. Similarly, for the other genera of the Vespertilioninae our study material has been drawn chiefly from specimens and to a much lesser extent from the published works of others. The specimens that we have examined are listed in Appendix 1. Our aim as far as genera other than *Pipistrellus* and *Eptesicus* are concerned has been to provide illustrations of representative bacula, but in those instances where bacular structure has not before been studied we have endeavoured to examine as many species within each genus as the available specimens permitted. Clearly, the material available to us has been quite inadequate to establish the extent of individual variation in any one species or subspecies. While only adult specimens (wing epiphyses fully fused) have been used, we have necessarily had to accept that for the majority of species our data is limited. We have concentrated therefore on studying and comparing the gross morphology (size, shape, gross structure) of the bacula that we have examined in an attempt to identify similarities, differences and general trends. The finer details perhaps more valuable in species distinction have received much less attention, although where it is known that species are difficult to separate by conventional means attention has been drawn to bacular features that may assist in identification.

The specimens used in this study have been drawn almost entirely from the collections of the British Museum (Natural History), London (BM(NH)) and the Harrison Zoological Museum, Sevenoaks, Kent (HZM). Apart from these we have been able to examine one from the Naturhistorisches Museum, Wien (NMW), by courtesy of Dr K. Bauer, and one from the Carnegie Museum of Natural History, Pittsburgh (CMNH), an anomalous specimen loaned for identification by Dr D. A. Schlitter, while Dr K. F. Koopman generously brought to London an example of *Nycticeius humeralis* from the American Museum of Natural History, New York (AMNH) from which a much needed baculum was obtained. Specimens prepared many years ago at the British Museum (Natural History) are dry, sometimes mounted on card: the remainder have been prepared in the course of this study. This has been accomplished by maceration for a short period in a 5% solution of potassium hydroxide to which a small quantity of alizarin red has been added, after which the grosser macerated tissue was removed by dissection, the specimen then being cleared and stored in glycerin.

Drawings have been prepared using either a stereoscopic microscope with graticule scale and attached camera lucida, or freehand using a similar instrument. A few were drawn freehand using a stereo projection microscope with travelling micrometer stage. The wide range of size variation among vespertilionine bacula (for example from a length of 1 mm or less to as much as 9 or 10 mm in *Pipistrellus*) has necessitated the use of several scales of magnification. So far as possible all drawings on any one page of figures are at the same magnification, with an appropriate scale: to facilitate comparison the varying magnifications used follow an arithmetic progression whereby each successive larger value is twice its predecessor. It has not always been possible to conform to this arrangement, especially where drawings have been prepared from published illustrations. As a rule dorsal (D) and right lateral (RL) views of each baculum are provided: rarely through damage the left lateral (LL) aspect is given. Occasionally where it is of especial interest a half ventral (RVL or LVL) drawing has been made, and in a few instances where drawings have been taken from the literature it has been necessary to give the ventral (V) rather than the dorsal aspect.

Authorship and responsibility

We take joint responsibility for the results and opinions put forward and expressed in this paper, and for the new names proposed therein.

The baculum of *Pipistrellus*

Four bacular types have been identified within the nominal genus *Pipistrellus*. With some exceptions, modification and combinations, these are in broad agreement with the groupings of species proposed by Tate (1942*a*) and Koopman (1973, 1975). The classifications of Tate and Koopman are summarised in Table 3.

(1) An elongate structure (Fig. 1a) with a slender shaft and paired basal flanges (e.g. Figs 2a–c, 3, 4, 5), the ventral surface of the proximal part of the shaft transversely concave, its distal part cylindrical or nearly so; in profile the base in line with the shaft or more or less deflected downward at an angle to it; the shaft may be more or less straight, flexed or variously curved in the vertical plane, while the tip is generally bifid or forked and may be directed ventrally to a greater or lesser extent.

Species aggregations in which this type of baculum is found include the *abramus, pipistrellus, coromandra* and *tenuis* groups of Tate (1942*a*); Koopman (1973) amalgamated these to form a *pipistrellus* group to which he added (1975) the African *nanus* and *permixtus*. However, *nanus* (Fig. 6b) proves to have a very different baculum, as does *imbricatus* (Fig. 9a), included by Tate in the *coromandra* group and thus by Koopman (1973) in the *pipistrellus* group. *Pipistrellus babu* (Fig. 4a), provisionally placed by Tate in the *kuhlii* group, also has the long, relatively straight baculum characteristic of this part of the division, as do *endoi* (Imaizumi, 1959) (Fig. 3b) and *peguensis* (Sinha, 1969) (Fig. 15c), both described since Tate wrote. The more recently described *westralis* (Koopman, 1984*c*) (Fig. 10d), *adamsi* (Fig. 10c) and *wattsi* (Fig. 10g) (Kitchener *et al.*, 1986) also belong with *tenuis* (Fig. 9d) and its allies in this grouping. Taxa referred to the *ceylonicus* group by both Tate and Koopman (1973) prove to have this bacular structure, as do those that have been examined of the *rueppellii* group (Figs 7e, f, 10a, b) of Koopman (1975). *Pipistrellus kuhlii* and its associates (Figs 5a–d, 6c) also belong in this division. In these, however, the basal lobes of the baculum are sharply angled to the shaft in the vertical plane, and this bacular profile is very characteristic of *kuhlii* and its relatives. The shaft is straight, without flexion, and the tip is usually bifid and not directed ventrally. Koopman (1975) included *anchietae* (Fig. 6e) in the *kuhlii* group, but this proves to have a very different bacular configuration.

A long-shafted baculum of this type occurs with little modification in the majority of the Australian species (Figs 11a–f, 12k) currently referred to *Eptesicus*, in *Nyctalus* (Fig. 10f), in *Scotozous* (Fig. 16d) (to which *rueppellii* and its immediate associates have sometimes been referred) and in *Scotoecus* (Fig. 20a–e), in which the 'horns' of the bifid tip extend in some instances almost to form a ring, a condition foreshadowed in *Pipistrellus paterculus* (Fig. 3c). The Australian *Scoteanax* (Fig. 16i) and *Scotorepens* (Figs 16g, h, 21e, f) also share this bacular type: in *Scoteanax* the 'horns' at the tip have become a transverse bar, but the species of *Scotorepens* retain the bifid or slightly bifid tip. A similar long-shafted baculum but with a simple tip occurs in the genera *Hesperoptenus* (Fig. 21a–c, g) and *Chalinolobus* (Fig. 17a–e). The baculum of *Glischropus* (Fig. 18a), although very small, is also of this type, with paired basal lobes, a slender shaft, and bifid tip.

(2) A very small structure (Fig. 1b), consisting of a broad base with two basal lobes (e.g. Figs 2d, e, 9c, h), supporting a short, very slightly hollowed shaft. This bacular type is found in *subflavus* (Fig. 2d), *circumdatus* (Fig. 2e), *societatis* (Fig. 9c) and the more recently described *cuprosus* (Hill & Francis, 1984) (Fig. 9h).

(3) A relatively short, stout shafted baculum (Fig. 1c), sometimes with expanded base and tip (e.g. Figs 6a, b, 7a, h, 8e, f), the base on occasion divided into paired lobes, sometimes angled vertically to the line of the shaft, which is fluted ventrally rather than mostly cylindrical; tip when expanded having its anterior edge sometimes divided into several irregular serrations and on occasion downwardly directed.

Such bacula are found in the *savii* group of Tate (1942*a*) and Koopman (1973, 1975) but not in *maderensis* (Fig. 5b) which was put into the *savii* group by both authors. Its baculum is however quite different and is like that of *kuhlii* and its associates. *Pipistrellus anchietae* (Fig. 6e), referred to the *kuhlii* group by Koopman (1975) also belongs with *savii,* and the same bacular type occurs in *nanus* (Fig. 6b), allocated with *permixtus* to the *pipistrellus* group by the same author. We have been unable to examine the baculum of *permixtus* but that of *nanus* and of *helios* (Fig. 6d) is of the type characteristic of this division, with its basal part quite sharply flexed to the shaft although not especially deep, and with an expanded, downwardly directed distal part. *Pipistrellus eisentrauti*

(Fig. 9g), referred to the *rueppellii* group by Koopman (1975) also shares this bacular type. The North American *hesperus* (Fig. 8d) was placed by this author in a *hesperus* group, with the African *musciculus*. It has a robust baculum of the type found in this division, somewhat flattened, without basal lobes but broadened just beyond the base, the shaft narrowing towards the tip; the ventral surface is shallowly fluted throughout its length. Unfortunately, no baculum has been available for *musciculus* but provisionally it is referred to this division on other grounds.

This bacular class also includes *imbricatus* (Fig. 9a), referred to the *coromandra* group by Tate (1942*a*) and by Koopman (1973), and *pulveratus* (Fig. 8c), *lophurus* (Fig. 8f), and *kitcheneri* (Fig. 8e) which Tate placed in the *affinis* group (vide infra). Koopman (loc. cit.) followed this lead with respect to *kitcheneri* but did not include *pulveratus* and *lophurus* since these were extralimital to his study. *Pipistrellus bodenheimeri* (Fig. 9f), described (Harrison, 1960) since Tate wrote and extralimital to Koopman (loc. cit., 1975) also belongs in this group. Tate referred *macrotis, vordermanni* and *curtatus* to the *savii* group on account of their reduced pm^2 but indicated that this allocation might not be tenable: however, the baculum of *macrotis* shows that it should be placed in this group. This author also created the *joffrei* group to include *joffrei, anthonyi, brachypterus,* and *stenopterus*: *brachypterus* has since proved to be a *Philetor* (Hill, 1971). We have been unable to examine the baculum in either *joffrei* or *anthonyi* but that of *stenopterus* (Fig. 7h) indicates that it belongs here. Both *joffrei* and *stenopterus* have been referred variously to *Nyctalus* (Chasen, 1940; Ellerman & Morrison-Scott, 1951) or to *Pipistrellus* (Tate, 1942*a*; Hill, 1966*a*) but the baculum of *stenopterus* has no resemblance to the long-shafted structure of the former genus.

(4) A relatively large, short but strong baculum (Fig. 1d), broad, with little or no proximal or distal expansion (e.g. Figs 8a, b, g, 10h), the ventral surface transversely deeply concave so that it is strongly arched or fluted throughout its length. This grouping includes *affinis* (Fig. 8a) and *petersi* (Fig. 8b), placed in the *affinis* group by Tate (1942*a*) and in the case of *petersi* in the same group by Koopman (1973), *affinis* being extralimital to his study, together with the Australian *tasmaniensis* (Fig. 8g) for which Tate maintained a *tasmaniensis* group. A further Australian form, *mackenziei* (Kitchener *et al.*, 1986) (Fig. 10h) is very like *tasmaniensis* and also belongs here. To some extent this grouping is linked to the previous division by *pulveratus, imbricatus, lophurus, kitcheneri* and their immediate associates: Tate allocated all except *imbricatus* to the *affinis* group.

The baculum of *Eptesicus*

We have been able to identify three bacular types among the species currently referred to the nominal genus *Eptesicus*. There is no single reference for species groupings in this aggregation of species, but for African forms these bacular types agree almost exactly with the species groups defined by Koopman (1975).

(1) A more or less triangular structure (Fig. 1e), its apex occasionally drawn out into a slight, short shaft, the base widened and sometimes slightly lobed but the tip not expanded, usually more or less pointed or gently rounded (e.g. Figs 13, 14a, c). This type of baculum is flattened, with little ventral fluting or concavity: there is little vertical flexion either of the base or of the more distal part, and the tip is not deflected downwards. So far as we have been able to establish, this bacular class occurs in all of the forms that are currently referred to *Eptesicus* from the New World, Europe and Asia, and in the African forms that Koopman (1975) included in the *serotinus* and *floweri* groups.

(2) The structure in a small group of species, wholly Australian, in which the baculum has usually a long cylindrical or slightly fluted shaft with paired expanded basal lobes (Fig. 1f) and usually a blunt tip (e.g. Fig. 11a–e), very similar in fact to the first of the bacular types that we have described for *Pipistrellus*. This grouping includes *pumilus* (Figs 11a, b, 12k), *vulturnus* (Fig. 11c), *douglasorum* (Fig. 11d) and *regulus* (Fig. 11e): in *pumilus* and *douglasorum* the shaft and base may be flexed rather like those of *Pipistrellus kuhlii* and its immediate relatives, while in *regulus* the shaft has an expansion just behind the tip (McKean *et al.*, 1978; Kitchener, 1976). A further species, *sagittula* (Fig. 11f), also appears to belong here, its baculum being perhaps a shorter-shafted version of this type.

(3) A slender-shafted baculum (Fig. 1g), usually with distinct paired basal lobes, sometimes angled or flexed to the line of the shaft, which is cylindrical, with variously expanded tip, the distal expansion varying from a downwardly directed spatulate plate to a large, anteriorly directed, downwardly deflected lobed structure (e.g. Figs 12a–j, 14b). Taxa with this type of baculum are wholly African and the grouping comprises those forms referred to the *capensis* and *tenuipinnis* group by Koopman (1975).

The baculum in other Vespertilioninae

Before considering the implications of bacular morphology in relation to the systematics of *Pipistrellus* and *Eptesicus*, a brief review of bacular types in the remaining genera of the Vespertilioninae will serve to place these nominal genera in the perspective of bacular structure in the subfamily as a whole.

Myotis (Fig. 19i, j). The baculum of *Myotis* has been figured and described by numerous authors. Palaearctic species have been studied by Topál (1958), Hanák (1965, 1970, 1971), Wallin (1969), Atallah (1970) and Baagøe (1973), among others. Nearctic and Neotropical species have been examined by Hamilton (1949), Wimsatt & Kallen (1952), Krutzsch & Vaughan (1955), Davis & Rippy (1968), Genoways & Jones (1969), LaVal (1973*a*) and Warner (1982). In this genus the baculum is much like a small saddle. In profile the base and tip are slightly elevated, the baculum ventrally slightly concave. In dorsal aspect the baculum is more or less triangular or projectile-shaped, anteriorly bluntly or sometimes more sharply pointed, the base divided to a greater or lesser extent into two lobes, the ventral surface deeply fluted. In some instances at least there is evidently distinctive variation between species and it is possible that some clear infrageneric division into bacular types might be made. There is also apparently considerable individual variation in some species, leading LaVal (1973*a*) in the case of *nigricans* to suggest the possibility that the material that he studied was a composite of sibling species. However, for so large a genus there seems to be a surprising degree of broad homogeneity in gross bacular structure. We have examined relatively few bacula from such a well known genus, but it is of some interest to note that the baculum of *ridleyi* (Fig. 19i), described and retained for many years in *Pipistrellus* on account of its dentition which corresponds to that genus (Hill & Topál, 1973) is undeniably of the type characteristic of *Myotis*.

Pizonyx (Fig. 19k). Figured and described by Hamilton (1949). The baculum is similar to that of *Myotis*, but lacks much of the saddle-like appearance, and is more triangular in dorsal aspect, tapering distally to a flattened, slightly elevated tip; it is also elevated proximally so that in profile the base inclines slightly upwards. Ventrally the baculum is slightly fluted.

Lasionycteris (Fig. 17f). Figured and described by Hamilton (1949). The baculum has a large, swollen, bilobed base, a long cylindrical shaft, and a slight distal enlargement, the tip and base elevated dorsally. Proximally, there is sometimes a flattened dorsal prominence on the base, its bilobed extremity projecting beyond the main bulbous part.

Plecotus (including *Corynorhinus*). The Old World forms (*Plecotus*, Figs 14d, 19g, h) are figured and described by Topál (1958), Lanza (1960) and Ibáñez & Fernández (1986), American taxa (*Corynorhinus*, Fig. 15f–h) by Nader & Hoffmeister (1983). In most the baculum is arrow-head-shaped, slightly saddle-like, with basal lobes and broad, short distal part, the base elevated dorsally, the ventral surface deeply fluted: in two taxa (*auritus*, Fig. 19g, *teneriffae*, Fig. 14d) it has a longer, more slender shaft with paired basal lobes and is less saddle-like.

Idionycteris (Fig. 15e). Figured and described by Nader & Hoffmeister (1983). An elongate baculum, with triangular basal plate, its apex directed posteriorly, and narrow shaft, curved dorsally and ventrally shallowly grooved.

Euderma. The baculum in this genus is so far apparently unknown.

Barbastella (Fig. 18j). Figured and described by Topál (1958). A small, saddle-like baculum similar in many ways to that of *Plecotus*, with elevated base, narrowed distal part which is upwardly curved, and with slightly raised, elevated tip.

Rhogeessa (Fig. 18k). Figured and described by LaVal (1973*b*). A small baculum with expanded, bilobed base and short, stubby shaft lacking any distal modification, the shaft ventrally fluted.

Baeodon (Fig. 15b). Figured and described by Brown *et al.* (1971) and LaVal (1973*b*). Baculum very like that of *Rhogeessa* but with shorter shaft.

Nycticeius. Australian forms hitherto referred to *Nycticeius* have been recognised as *Scoteanax* and *Scotorepens* by Kitchener & Caputi (1985). As therefore it is currently understood, *Nycticeius* includes two species, *humeralis* from North America and *schlieffenii* from Africa. These have widely differing bacula. In *humeralis* (Fig. 17k) the baculum is blade-like, with short, narrow shaft, the base thickened, proximally forming a prominent angle which inclines towards the ventral surface, the distal portion deep, with convex walls which terminate in an ascending point. This structure is figured by Hamilton (1949) who remarked that it differed markedly from the bacula of other [North American] genera: in fact it is not closely approached by any other vespertilionine. The baculum of *schlieffenii* (Fig. 16e), by contrast, has a broad bilobed base with tapering, fluted shaft, its tip unmodified, bluntly pointed, and unexpanded. Moreover, the bacular morphology of the Australian species formerly referred to *Nycticeius* supports their separation from this genus. This matter is discussed more fully below.

Otonycteris (Fig. 16a). Figured and described by Wassif & Madkour (1972), Fairon (1980) and Wassif, Madkour & Soliman (1984). An unusual baculum, mostly a more or less parallel-sided narrow shaft, the base and tip not expanded, both strongly elevated dorsally, the shaft tapering distally to a raised tip.

Lasiurus (Fig. 19l). Figured and described by Hamilton (1949). A slipper-like baculum with broad, dorsally elevated base, a short shaft, fluted ventrally, and with slightly expanded and elevated tip.

Dasypterus (Fig. 18f). Figured and described by Brown *et al.* (1971) and Hamilton (1949). Baculum like that of *Lasiurus* but tip as a rule not upturned.

Antrozous (Fig. 18b). Figured and described by Krutzsch & Vaughan (1955) and Pine *et al.* (1971). Baculum broadly triangular in dorsal view, tapering to broad, blunt point, fluted ventrally, and with the base elevated dorsally. It is very different from the baculum in *Nyctophilus* and *Pharotis*, and from that of *Otonycteris*, with which genera *Antrozous* has been associated in the past.

Bauerus (Fig. 15i). Figured and described by Pine *et al.* (1971). Baculum like that of *Antrozous* but smaller and narrower, the distal part not upcurved.

Scotomanes (Fig. 18g). A short baculum with broad, bilobed base merging into a very narrow, short cylindrical shaft with no distal expansion, lacking any upward deflection either proximally or distally.

Scotophilus (Fig. 17g–j). Figured and described by Harrison & Brownlow (1978). Baculum irregularly sub-rectangular or sub-triangular, flattened, anteriorly usually bluntly rounded, slightly concave in ventral transverse section, with slight basal lobes.

Vespertilio. Figured and described by Topál (1958) and Wallin (1969). In two species (*murinus* and *orientalis*) the baculum is situated at the base of the penis, which is supported by a cartilaginous pseudobaculum. In the third (*superans*) the baculum is situated not at the base of the penis but midway along the shaft, and there is no pseudobaculum. The baculum in *orientalis* (Fig. 21j) and *superans* is flattened and triangular, with a broad, bilobed base, tapering anteriorly to a narrow point and with slight vertical flexion. The baculum of *murinus* (Fig. 21i) is broad but less triangular in outline, and has a wide, bluntly rounded distal part. The bacula of *orientalis* and *superans* in particular are similar in many respects to those of the *Eptesicus serotinus* group (vide supra).

Histiotus (Fig. 18c–e). A very small baculum, with expanded bilobed base and short, narrow cylindrical shaft, its tip unexpanded, the base and tip deflected slightly upwards.

Ia (Fig. 21d). Figured and described by Topál (1970*a*). A large, flattened, triangular baculum similar to those of the *Eptesicus serotinus* group (vide supra).

Tylonycteris (Fig. 18h, i). Baculum small, similar to that of *Histiotus* or to those of the *Eptesicus serotinus* group (vide supra), but with the distal part extended into a narrowed shaft and with relatively wider, expanded base with a slight trace of basal lobes.

Glauconycteris (Fig. 19a–f). Baculum very small and somewhat variable within the genus, but mostly more or less triangular, with some modification, usually as reduction, to a deeply lobed base with a short, blunt distal portion. However, on occasion the base is slightly or considerably expanded and the distal portion lengthened to a short shaft.

Mimetillus. We have been unable to establish the presence of a baculum in this monotypic genus, from which it appears to be lacking.

Eudiscopus. The baculum of *Eudiscopus* (if present) is apparently unknown.

Nyctalus (Fig. 10f). Figured and described by Topál (1958) and Lanza (1959). A long, slender baculum with narrow basal lobes, a long cylindrical shaft, and slightly bifurcated tip.

Laephotis (Fig. 16f). Baculum with expanded, bilobed base, narrow fluted shaft and broadly expanded tip with slight downward deflection, a small protuberance on its upper surface. Similar in many respects to the baculum in the *Eptesicus capensis* and *E. tenuipinnis* groups (vide supra).

Glischropus (Fig. 18a). A very small baculum, with paired basal lobes, narrow cylindrical shaft and slightly expanded, bifid tip.

Scotozous (Fig. 16d). Figured and described by Sinha (1976). A long baculum with slight basal lobes, a narrow, fluted shaft, and slightly bifid tip, the shaft slightly flexed.

Scoteanax (Fig. 16i). Figured and described by Kitchener & Caputi (1985). A long baculum with strong, expanded bilobed base, a slender cylindrical shaft, and with the tip embellished into a short, transverse bar.

Scotorepens (Figs 16g, h, 21e, f). Figured and described by Kitchener & Caputi (1985). A long baculum with expanded, bilobed base and slender, cylindrical shaft, the tip slightly expanded and bifid, the 'horns' deflected ventrally.

Scotoecus (Figs 20a–e, 21h). A long, slender baculum with slightly expanded and bilobed base, long cylindrical shaft and an expanded, bifurcated tip, the 'horns' extending ventrally and sometimes curving to form an almost complete ring.

Philetor (Fig. 16b). Figured and described by Hill (1966*a*). A strong but relatively short baculum with paired basal lobes, a short, fluted shaft, and expanded rugose tip, the base and tip elevated and deflected upwards.

Hesperoptenus (Fig. 21a–c, g). Figured and described by Hill (1976) and Hill & Francis (1984). Baculum long and slender, with paired basal lobes, a flattened, ventrally fluted shaft, and unmodified, rounded tip.

Chalinolobus (Fig. 17a–e). Baculum long, with clearly defined basal lobes, a long cylindrical shaft, and an expanded tip, the expansion sometimes slight, considerable, or bifid with two obtuse projections.

Although the two genera are commonly referred to a separate subfamily, the Nyctophilinae, for purposes of comparison we have also examined the baculum in *Nyctophilus* and *Pharotis*.

Nyctophilus (Figs 16c, 22a–g). Figured by Churchill *et al.* (1984). A long, rather broad baculum with scarcely expanded, bilobed base and a broad shaft tapering distally to a blunt point, or wider terminally with a median emargination to produce a shallowly bifid tip; shaft ventrally deeply fluted.

Pharotis (Fig. 22h). Baculum similar to that of *Nyctophilus* but shaft narrower, tapering to slightly expanded tip.

Systematic considerations

The majority of genera in the Vespertilioninae have bacula which overall display a wide range of variation in their gross morphology. Most have a distinctive baculum: where closely similar bacula occur in genera currently recognised as distinct, as for example in *Scotozous* and *Pipistrellus,* then close relationship has been presumed on other morphological grounds. We are thus persuaded that in this subfamily the baculum can be used as a guide to infrageneric and intergeneric classification, although it seems that its value as a suprageneric indicator may be less. In the same way, although we have not explored the point in detail, it has become apparent that in many genera the minor details of bacular morphology can be used to assist in species distinction. These considerations have led us to the view that the very dissimilar bacular types that we have been able to identify and define within *Pipistrellus* and *Eptesicus* do indeed reflect natural groupings and show that *Eptesicus* as it is currently defined is a composite. Certainly it seems true to say that the current classification of both nominal genera does not properly reflect the relationships that we believe bacular morphology suggests exist within and between them.

Genus *Pipistrellus* Kaup, 1829

Pipistrellus Kaup, 1829: 98. *Vespertilio pipistrellus* Schreber.
Romicia Gray, 1838: 495. *Romicia calcarata* Gray = *Vespertilio kuhlii* Kuhl.
Romicius Blyth, 1840: 75. Variant of *Romicia* Gray.
Hypsugo Kolenati, 1956: 131. Included *Vespertilio maurus* Blasius = *Vespertilio savii* Bonaparte, and *Vespertilio kraschenninikowii* Eversmann. Type species fixed as *Vespertilio savii* Bonaparte by Wallin (1969). Valid as a subgenus.
Nannugo Kolenati, 1856: 131. Included *Vespertilio nathusii* Keyserling & Blasius, *Vespertilio kuhlii* Kuhl and *Vespertilio pipistrellus* Schreber.
Alobus Peters, 1868: 707. *Vespertilio temminckii* Cretzschmar = *Vespertilio ruppellii* Fischer. Preoccupied by *Alobus* Le Conte, 1856 (Coleoptera).
Euvesperugo Acloque, 1899: 35. Included six species, one being *Vespertilio pipistrellus* Schreber.
Eptesicops Roberts, 1926: 245. *Scotophilus rusticus* Tomes.
Neoromicia Roberts, 1926: 245. *Eptesicus zuluensis* Roberts. Valid as a subgenus.
Vansonia Roberts, 1946: 304. *Pipistrellus vernayi* Roberts = *Vespertilio ruppellii* Fischer.
Vespadelus Iredale & Troughton, 1934: iii, 95. *Scotophilus pumilus* Gray. Nomen nudum.
Vespadelus Troughton, 1943: 348. *Scotophilus pumilus* Gray. Valid as a subgenus.
Registrellus Troughton, 1943: 349. *Pipistrellus regulus* Thomas (see Hill, 1966*b*).
Falsistrellus Troughton, 1943: 349. *Vespertilio tasmaniensis* Gould. Valid as a subgenus.
Perimyotis Menu, 1984: 409, 415. *Vespertilio subflavus* F. Cuvier. Valid as a subgenus.
Parastrellus Horáček & Hanák, 1985*a*: unpaginated; 1985*b*: 62; 1985–1986: 15, fig. 4. *Pipistrellus hesperus* H. Allen. Nomen nudum.

The genus *Pipistrellus* cannot be diagnosed by conventional morphological characters that are individually exclusive. Its current definition rests on Miller (1907) who based his diagnosis on the structure of i^2 which is simple or has a well developed secondary cusp; on the reduction of i^3 which is smaller than i^2 but nevertheless extends beyond the cingulum of that tooth; on rather short canines, c^1 often but not invariably with incipient secondary cusp on its posterior edge; and on the absence of $pm\frac{3}{3}$ to give the dental formula $i\frac{-23}{123}$, $c\frac{1}{1}$, $pm\frac{-2-4}{-2-4}$, $m\frac{123}{123} = 34$, with pm^2 barely or not in the toothrow. He remarked that the members of the genus were recognisable by their dental formula, large i^3, unmodified skull and ears, and the normally long fifth finger.

The definition of the genus is briefly discussed by Tate (1942*a*), Ellerman & Morrison-Scott (1951) and Kitchener *et al.* (1986). All recognised the unreliability of the presence or absence of pm^2 as a prime diagnostic character, Ellerman & Morrison-Scott also remarking that ‘strictly speaking *Pipistrellus* is not more than a subgenus of *Eptesicus*, which itself might be referred to *Vespertilio'*, but for convenience they and most other recent authors have followed the conventional distinction. It is clear from the foregoing account of the baculum in the Vespertilioninae that the species allocated to *Pipistrellus* can be separated from most other vespertilionine genera by their bacular morphology: those genera which have bacula similar to those of some *Pipistrellus* species (e.g. *Nyctalus, Scotozous*) can be defined by other morphological features of the skull and dentition, as they were by Miller (loc. cit.).

Species groups in *Pipistrellus* are difficult and in some instances almost impossible to define on external, cranial and dental characters: most (Tate, 1942*a*; Koopman, 1973, 1975) are brought together by combinations of characters with few or sometimes no exclusive features. Some species of *Pipistrellus*, moreover, appear difficult to separate from some of *Eptesicus* (Koopman, 1975; Heller & Volleth, 1984) except by the presence or absence of pm^2 which is itself evanescent. Bacular morphology appears to offer at least a partial solution to this difficulty, at the same time indicating that the genus as currently understood is a composite of several different groups of species, as suggested by Heller & Volleth (loc. cit.) on the basis of its known karyology.

Chromosomal features so far as they have been established in *Pipistrellus* are reviewed by Heller & Volleth (1984) and Zima & Horáček (1985). Their summaries demonstrate that karyologically *Pipistrellus* as currently constituted is a very heterogeneous and diverse group, with 2N varying from 26–44 and FN from 44–60. At this stage we have been unable to find any consistent correlation between the chromosome formulae that these authors quote for various species and the groupings that we recognise on bacular and other grounds. However, many species remain to be studied karyologically and it appears from Zima & Horáček that for the present karyotype variability in the Vespertilioninae may be only of limited value as a taxonomic criterion.

While at present we would not support the generic division of *Pipistrellus* as has been indicated or suggested by Menu (1984), Horáček & Hanák (1985*a*, *b*) or Kitchener *et al.* (1986) since besides bacular features there appear to be few or no characters reported for its constituent groups that would support this wider separation, we consider that the divisions apparent within the genus justify subgeneric recognition. Wallin (1969) has already anticipated this view to some extent, employing *Hypsugo* Kolenati, 1856 for *P. savii*, in part on bacular grounds. Horáček & Hanák (1985–1986) recognised *Hypsugo* as a distinct genus. The gross morphology of the baculum also indicates that the Australian taxa formerly referred to *Eptesicus* should be transferred to *Pipistrellus*, as Heller & Volleth (1984) suggested, and that the African forms hitherto allocated to the *capensis* and *tenuipinnis* groups of *Eptesicus* also represent *Pipistrellus* as these authors inferred on account of their known karyology. Thus we would classify *Pipistrellus* in the following manner, listing included taxa without distinction as to taxonomic rank: some are not necessarily valid species or subspecies and for obvious reasons we have been unable to examine every named form in the genus.

Subgenus ***Pipistrellus*** (***Pipistrellus***)

Baculum long, with strong, extended shaft, well developed basal lobes, nearly always with a bifid tip. Braincase high, rounded, not flattened, sometimes globose; postorbital region usually wide; cranial profile generally straight or nearly straight from occiput to nares; interdental palate longer than wide; maxillary toothrows parallel or only slightly convergent anteriorly; i^2 generally bicuspid; pm^2 usually large, pm_2 not greatly reduced, usually about 3/4 crown area of pm_4. *Pipistrellus kuhlii* and its associates differ slightly in almost unicuspid i^2; greatly reduced i^3, much reduced pm^2 and more reduced pm_2 although some of these features occur in isolation in other species of the subgenus.

(*a*) ***pipistrellus*** group
Basal lobes of baculum more or less in line with the bacular shaft in the vertical plane; i^2 bicuspid, but not strongly so, cusps not deeply divided.

(*a*) (i) *pipistrellus* subgroup. Braincase high, rounded; postorbital region wide; supraorbital region not widened or swollen; rostrum long, not greatly broadened, with shallow median rostral depression; cranial profile almost straight from occiput to nares, slightly depressed over anterior part of orbit; premaxillae not shortened; zygomata slender, lacking any jugal eminence; interdental palate longer than wide; maxillary toothrows parallel for most of their length, anteriorly slightly convergent; short bony post-palate; slight basial pits; i^2 bicuspid, posterior cusp 1/2–3/4 the height of anterior cusp; i^3 about the same in crown area or a little larger than i^2, about 1/2 or a little more its height, with larger central and smaller lateral accessory cusps, lying postero-externally to that tooth, separated from c^1 by a small diastema; pm^2 large, unreduced, its crown area similar to that or i^2 or a little less, slightly intruded but separating c^1 and pm^4; i_{1-3} not much imbricated, i_3 about twice the bulk of i_{1-2}; pm_2 not usually much reduced, about 1/2–3/4 or more the crown area of pm_4.

Included taxa: *aladdin, bactrianus, lacteus, nathusii* (Fig. 2b); *mediterraneus*, (?) *permixtus, pipistrellus* (Fig. 2a).

Among African *Pipistrellus* we have been unable to examine the baculum of *permixtus* (Aellen, 1957) compared by its describer chiefly with *nathusii*. Its dentition, with bicuspid i^2, the posterior cusp 2/3 the height of the anterior cusp, i^3 with lateral accessory cusps, its main cusp equal in height to the posterior cusp of i^2, large, slightly intruded pm^2 which is about as big as i^3, and unreduced pm_2, its crown area about 3/4–4/5 the crown area of pm_4 suggests that it should be referred to the *pipistrellus* subgroup. Koopman (1975) referred it to the *pipistrellus* group.

(*a*) (ii) *javanicus (abramus)* subgroup. Braincase slightly globular, elevated posteriorly; postorbital region wide; supraorbital region distinctly broadened to produce abruptly incurving lateral margins to the anterior part of the postorbital area; rostrum broad, dorsally flattened, with no more than an indication of a median rostral depression; cranial profile almost straight from occiput to nares, slightly flattened over the occiput and a little depressed over the anterior part of the orbits; premaxillae not shortened; zygomata slender but not weak, lacking any jugal eminence; interdental palate only little longer than wide; palate strongly domed with broad anterior emargination; maxillary toothrows more or less parallel, scarcely convergent anteriorly; short bony post-palate; shallow basial pits; i^2 well developed, bicuspid, posterior cusp sometimes small, usually about 3/4 height of anterior cusp; i^3 similar in size to i^2 or slightly larger, about as high as its posterior cusp, with larger central and smaller lateral accessory cusps, lying postero-externally to that tooth, separated from c^1 by a narrow diastema; pm^2 little reduced, equal to or rather less than i^3 in crown area, in recess between c^1 and pm^4 which approach but do not touch; i_{i-3} scarcely imbricated, i_3 as a rule similar in size to i_2, both a little more massive than i_1; pm_2 about 1/2–3/4 the size of pm_4, very slightly intruded from toothrow.

Included taxa: *abramus* (Fig. 3a), *akokomuli, babu* (Fig. 4a), *bancanus, camortae* (Fig. 15d), *endoi* (Fig. 3b), *irretitus, javanicus* (Fig. 10e), *meyeni, peguensis* (Fig. 15c), *paterculus* (Fig. 3c), *pumiloides*.

Current treatments of Asian *Pipistrellus* usually include *abramus* in *P. javanicus* (*tralatitius*, Laurie & Hill, 1954) as a valid subspecies. There appear to be few conventional features that clearly separate *javanicus* from *abramus* but their bacula differ quite sharply in the high degree of vertical flexion of the shaft evident in the latter. This difference was used by Thomas (1928*a*) who examined Indo-Chinese *Pipistrellus* and differentiated *abramus* from *raptor, javanicus* (as *tralatitius*) and *coromandra* by virtue of the double curvature of its baculum, the others being straight. Van Peenen *et al.* (1969) recorded *coromandra, javanicus* and *mimus* from Vietnam but the baculum that they illustrate for *javanicus* is clearly that of *abramus*. This bacular difference suggests that *javanicus* and *abramus* should be considered specifically distinct even although there seem to be few cranial and dental characters to separate them. The braincase in *javanicus* is slightly more inflated than in *abramus* and its rostrum narrower, the palate is usually a little wider in relation to its length and is slightly more excavated and domed, while pm^2 is a little less reduced and less intruded, tending rather more to separate c^1 and pm^4. Both occur in Vietnam (Thomas, 1928*a*; specimens listed below). It seems likely that *bancanus* and *camortae*, which has an unflexed baculum, are more closely related to *javanicus* than to *abramus*.

Soota & Chaturvedi (1980) remarked that Thomas (1915*c*) had pointed out that the baculum of *abramus* is doubly curved and that in *paterculus* it is straight, but they stated further that material of *paterculus* in the collections of the Zoological Survey of India revealed that its baculum is doubly curved. However, specimens in the collections of the British Museum (Natural History) referred to *paterculus* (some the original material seen by Thomas) have relatively straight bacula when compared with the sinuous baculum of *abramus*. We have found this sinuous baculum to be characteristic of *abramus*, to which perhaps the specimens seen by Soota & Chaturvedi should be referred.

The very elongate baculum of *paterculus*, with its strongly bifid tip, the 'horns' of which are deflected ventrally and extend to some extent to form a ring (Thomas, 1915*c*) is reminiscent of the baculum of *Scotoecus*. A very long baculum is also found in *endoi*, but in this species the tip is less strongly bifid and the 'horns' are deflected dorsally. Both, however, are clearly referable to *Pipistrellus* on cranial and dental characters, *Scotoecus* being distinguished especially by a massive unicuspid i^2, the loss of i^3, a grooved c^1, and usually by the absence of pm^2.

(*a*) (iii) *coromandra* subgroup. Small, with small, rounded braincase, elevated posteriorly and slightly so frontally; postorbital region wide; rostrum short, relatively narrow; no median rostral depression; cranial profile straight or nearly so from occiput to tip of rostrum; premaxillae exceptionally short; zygomata slender, without jugal projection; interdental palate about as long or a little longer than wide; short bony post-palate: no basial depressions; i^2 usually bicuspid, posterior cusp sometimes very small or rarely absent, when present about 1/2 or a little more the height of the anterior cusp; i^3 equal or greater than i^2 in crown area, reaching to tip of its posterior cusp, with larger principal cusp and smaller lateral accessory cusps, lying postero-externally to the inner tooth; pm^2 not much reduced, nearly as great or as great in crown area as i^3, with well developed, slightly inwardly directed pointed cusp, in recess between c^1 and pm^4; i_{1-3} not much imbricated, i_3 a little larger than i_{1-2}; pm_2 about 1/2 crown area and height of pm_4, slightly extruded.

Included taxa: *adamsi* (Fig. 10c), *afghanus, angulatus, collinus* (Fig. 4b), *coromandra* (Fig. 7c), *glaucillus, mimus* (Fig. 7g), *murrayi* (Fig. 4c), *nitidus, papuanus* (Fig. 2c), *ponceleti* (Fig. 4d), *portensis, principulus, sewelanus, sturdeei*; possibly *subulidens* which may however represent *javanicus*; *tenuis* (Fig. 9d), *tramatus* (Fig. 7b), *wattsi* (Fig. 10g), *westralis* (Fig. 10d).

(*a*) (iv) *ceylonicus* subgroup. Large, with rather short, broad braincase; wide postorbital region; some degree of supraorbital expansion; rostrum broad, rather long; weak, diffuse median rostral depression; cranial profile slightly convex, raised over the frontal region; premaxillae normal, not shortened; zygomata moderate, without jugal eminence or process, interdental palate longer than wide; maxillary toothrows parallel; short bony post-palate; slight basial pits; i^2 large and massive, bicuspid to almost unicuspid, with moderate to small posterior cusp about 2/3 height of anterior cusp; i^3 massive, as large or larger than i^2, extending to or a little beyond posterior cusp of that tooth, with large principal cusp and smaller lateral accessory cusps, lying postero-laterally to i^2, narrowly separated from c^1; pm^2 large, nearly as great or greater in crown area than i^3, usually filling the recess between c^1 and pm^4 into which it is intruded, these almost in contact labially; i_{1-3} slightly imbricated, i_3 a little larger than i_{1-2}; pm_2 almost as large in crown area as pm_4, very slightly extruded from the toothrow.

Included taxa: *borneanus, ceylonicus* (Fig. 7d), *chrysothrix, indicus*, (?) *minahassae, raptor* (Fig. 3d), *shanorum, subcanus*.

An account of *minahassae* is given by Tate (1942*a*) who referred it to a *minahassae* group of which it was the sole member. The skull of the holotype has never been described and Tate's remarks are based on a referred specimen in the American Museum of Natural History, New York (AMNH 102359). It has a short, high braincase with rudiments of a sagittal crest, prominent supraorbital tubercles and slender zygomata; i^2 is long, with well developed posterior cusp, c^1 slender, lacking an accessory cusp, pm^2 only slightly intruded, its crown area greater than that of i^3, and i_{1-3} scarcely imbricated. These features suggest that if this specimen represents *minahassae* the taxon should be allocated to *Pipistrellus (Pipistrellus)* and provisionally we place it in the *ceylonicus* subgroup of the *pipistrellus* group, but clearly these decisions can only be speculative.

(*b*) ***rueppellii*** **group**

Baculum as in *pipistrellus* group; braincase high, broadened, rounded and globose; postorbital region wide; supraorbital region slightly expanded; rostrum short; with shallow, ill-defined median depression; cranial profile almost straight, a little raised over frontal region, a little depressed over rostrum; premaxillae not shortened; zygomata slender, without jugal projection; interdental palate a little longer than wide; maxillary toothrows slightly convergent; short bony post-palate; no basial pits, instead a shallow depression; i^2 strongly bicuspid, posterior cusp about 3/4 height of anterior cusp; i^3 usually very small or minute, its crown area less than 1/2 that of i^2, its tip sometimes barely rising above the cingulum of the inner tooth, on occasion (e.g. *nanulus*) larger, equal to or slightly exceeding i^2 in crown area, about 1/2 or a little more the height of that tooth; i^3 lying sublaterally to i^2, separated from c^1 by a wide diastema; pm^2 not usually greatly reduced, its crown area similar to that of i^2, with strong cusp, separating c^1 and pm^4, occasionally (*crassulus*) much reduced, similar in size to i^3 in its much reduced condition, or (*crassulus, nanulus*) recessed between these teeth; i_{1-3} little imbricated, i_3 slightly the largest as a rule; pm_2 about 3/4 or more as large in crown area as pm_4 and about 3/4 its height, rarely (*coxi, crassulus*) more reduced, about 1/2 crown area and height of pm_4.

Included taxa: Probably *coxi*; *crassulus* (Fig. 7e), *fuscipes, leucomelas, nanulus* (Fig. 7f), *pulcher* (Fig. 10a), *rueppellii* (Fig. 10b), *senegalensis, vernayi*.

Vansonia Roberts, 1946 is available should further separation of the *rueppellii* group be thought justified: an earlier name, *Alobus* Peters, 1867 is preoccupied.

(*c*) ***kuhlii*** group

Baculum of moderate length with narrow cylindrical shaft and paired basal lobes as in *pipistrellus* and *rueppellii* groups but basal lobes strongly angled to line of shaft in vertical plane; braincase low but not flattened, rounded, only slightly elongate; postorbital region wide; supraorbital region not widened or swollen; rostrum long, unwidened, with very slight median flattening; cranial profile almost straight from occiput to nares, slightly raised over frontal region, slightly depressed over front of orbits; premaxillae slightly shortened; zygomata slender, weak, without jugal eminence; interdental palate longer than wide; maxillary toothrows almost parallel; short bony post-palate; small, narrow basial pits; i^2 usually unicuspid, at best only slightly bicuspid; i^3 small, its crown area 1/2 or less that of i^2, its tip extending only slightly beyond the cingulum of that tooth, to which it lies laterally or sublaterally, separated from c^1 by a moderate or narrow diastema; pm^2 small, similar in crown area to i^3, intruded to lie in recess between c^1 and pm^4, these more or less in contact; i_{1-3} moderately imbricated, i_3 slightly the largest; pm_2 reduced, about 1/2 or less the crown area and height of pm_4.

Included taxa: Probably *aero*; *deserti* (*aegyptius*, Qumsiyeh, 1985) (Fig. 5c), *fuscatus, ikwanius*; probably *inexspectatus*; *kuhlii* (Fig. 5a), *maderensis* (Fig. 5b), *marrensis, rusticus* (Figs 5d, 6c).

We have been unable to examine the baculum of *inexspectatus* (Aellen, 1959) but this taxon was placed in the *kuhlii* group by Koopman (1975) who also referred *maderensis* to the *savii* group. However, an example of *maderensis* in the collections of the British Museum (Natural History) has a baculum clearly of the *kuhlii* type.

Romicia Gray, 1838 is available for the *kuhlii* group should this be thought worthy of further separation.

Subgenus ***Pipistrellus (Vespadelus)***

Baculum usually with long cylindrical or ventrally slightly fluted shaft, paired basal lobes and a blunt tip; shaft shorter and wider in *sagittula*; basal lobes sometimes flexed to line of shaft in vertical plane; braincase slightly broadened, flattened and elongated; postorbital region wide; supraorbital region slightly broadened; rostrum short but not greatly widened; shallow median rostral depression; cranial profile almost straight from occiput to nares, a little depressed over rostrum; premaxillae not shortened; zygomata slender, without jugal process; interdental palate a little longer than wide; maxillary toothrows slightly convergent anteriorly; short bony post-palate; no basial pits: i^2 bicuspid, posterior cusp almost as high as anterior cusp; i^3 much reduced, its crown area 1/2 or less that of i^2, its tip barely extending beyond the cingulum of that tooth, to which i^3 lies postero-laterally, separated from c^1 by a narrow diastema; pm^2 almost invariably absent, when present a small spicule in recess between c^1 and pm^4: i_{1-3} moderately imbricated, i_3 slightly the largest, pm_2 greatly reduced, in crown area about 1/2 or more usually less the crown area of pm_4, and 1/2 its height.

Included taxa: *caurinus* (Fig. 11b), *douglasorum* (Fig. 11d), *pumilus* (Figs 11a, 12k), *regulus* (Fig. 11e), *sagittula* (Fig. 11f), *vulturnus* (Fig. 11c).

Formerly referred to *Eptesicus*, the transfer of these taxa to *Pipistrellus* was first suggested by Heller & Volleth (1984), purely on bacular grounds. The bacular, cranial and dental features of this group suggest that it represents *P.* (*Pipistrellus*) in Australia, the few members of this subgenus (*adamsi*, *westralis* and perhaps *javanicus*) that also occur there being possibly slightly less differentiated by virtue of their relatively slightly less shortened skulls and their retention of pm^2. The *pipistrellus* group of the subgenus extends widely through the islands of Indo-Australia to New Guinea, the Solomon Islands and Australia, chiefly as the *coromandra* subgroup, to which *adamsi* and *westralis* belong. The *javanicus* subgroup reaches at least to Java and Sulawesi and may extend to Australia (Hill, 1983) but the Australian record of *javanicus* is based on two old examples and has never been confirmed. Possibly the slightly differentiated *pumilus* and it allies result from a further perhaps earlier invasion of Australia. Bacular differences in this subgenus (Figs 11, 12k) suggest that it may consist of two groups: it has been possible to examine only *pumilus*.

There has been hitherto a wide geographical hiatus in the Indo-Australian distribution of *Eptesicus* as formerly understood. Beyond these Australian forms, no other taxon attributed to this nominal genus has been reported further east in Indo-Australia than southern Thailand, other than an unconfirmed record from Sarawak of *Eptesicus* sp. (Pirlot, 1968) which provided no details.

Subgenus ***Pipistrellus (Perimyotis)***

Baculum very small, Y-shaped, with paired basal lobes and very short shaft; braincase slightly elongate, rounded, almost globose; postorbital region wide; supraorbital region slightly broadened; rostrum long, elevated, slightly widened; shallow median frontal depression; a very slight lateral depression on each side just anterior to the orbital rim; cranial profile sinuous, raised over frontal region, a little depressed over front of orbits; premaxillae not shortened; zygomata moderate, a slight jugal eminence; interdental palate longer than wide with wide anterior palatal emargination; maxillary toothrows convergent anteriorly; very short bony post-palate; slight basial depressions; i^2 bicuspid with well developed posterior cusp about 3/4 height of anterior cusp; i^3 massive, its crown area exceeding that of i^2, in height reaching or exceeding the height of anterior cusp of that tooth, with larger principal cusp and smaller lateral accessory cusps, lying postero-externally to inner tooth, separated from c^1 by a wide diastema; pm^2 large, its crown area equal to that of i^3, in toothrow, sometimes separated from pm^4 by a slight diastema; i^{2-3} and pm^2 almost identical to those of *P. nathusii*; i_{1-3} not imbricated, i^3 only slightly bulkier than i_{1-2}; pm_2 not greatly reduced or compressed in toothrow, its crown area about 1/2 or more that of pm_4, about 1/2–3/4 its height; tragus myotine, about 1/2 height of ear, tapering to blunt point.

Included taxon: *subflavus* (Fig. 2d).

Menu (1984) proposed the genus *Perimyotis* for *P. subflavus*, chiefly on account of the features of the canine and post-canine dentition in which he believed this species to approach *Myotis*. However, Hill & Topál (1973) in discussing *Myotis rosseti* and *M. ridleyi* which also combine the tragal features of *Myotis* with the *Pipistrellus* dentition ($pm\frac{3}{3}$ absent) noted that in *Myotis* i^2 is short and broad, its posterior cusp wider basally than the anterior cusp, while in *Pipistrellus* this tooth is linear, often narrower posteriorly than anteriorly. Also, in *Myotis* the principal cusp of i^3 is equal to or exceeds that of i^2 in height and the tooth is often hooked to produce a caniniform apperance while in *Pipistrellus* it is lower and is not hooked. In *Myotis* i_3 is usually much larger than i_{1-2} but in *Pipistrellus* there is as a rule no such great distinction in size. The incisive dentition of *subflavus* corresponds closely with that of *Pipistrellus*.

The baculum of *subflavus* is of a type not found in *Myotis*. Menu (1984) stated on the basis of published figures that the baculum approached that of certain *Myotis* and more particularly that of *Plecotus auritus*. We find no significant resemblance to the morphologically rather stable, saddle-like baculum of *Myotis* and although there are some similarities with the bacula of *Plecotus auritus* (Fig. 19g) and *P. teneriffae* (Fig. 14d), that of *P. austriacus* (Fig. 19h) is nearer in structure to the myotine baculum. The bacular type found in *subflavus* occurs in a similar form in *Pipistrellus circumdatus* (Fig. 2e), *P. societatis* (Fig. 9c) and *P. cuprosus* (Fig. 9h). There are considerable differences, however, between *subflavus* and *circumdatus* and its allies, not least in the degree of reduction of pm^2, this tooth in these three species being very small or absent.

The unshortened rostrum and the dental features of *subflavus* suggest that it is nearest to *P. (Pipistrellus)*, which it appears to represent in North America. We find *hesperus*, the other North American species of *Pipistrellus*, to belong on bacular and dental grounds to *P. (Hypsugo)*. Thus we do not support Menu's view (p. 410, footnote) that *Pipistrellus* is limited to the Old World and that the lines leading to this genus did not enter the North American continent. The marked differences between *subflavus* and *hesperus* indicate two quite different pipistrelline groups, as Hamilton (1949) remarked in relation to their bacula, but bacular and dental evidence suggests alliance to established Old World groupings, the baculum of *subflavus* being perhaps a reduced form of the shafted structure found in *P. (Pipistrellus)*, that of *hesperus* a modification of the type found in *P. (Hypsugo)*.

Subgenus *Pipistrellus (Hypsugo)*

Baculum usually short, stout, sometimes with expanded base and tip; base rarely bilobed, sometimes dorsally elevated; shaft generally flattened dorso-ventrally, sometimes wide, its underside transversely concave or fluted; tip ventrally hollowed as an extension of ventral fluting of shaft, when expanded anteriorly sub-square or slightly rounded, its anterior edge sometimes irregularly serrated, tip sometimes downwardly directed, its lateral margins on occasion forming two broadly based, ventrally directed projections; pm^2 generally much reduced, small, minute, or rarely absent.

Wallin (1969) considered *Hypsugo* a valid subgenus within *Pipistrellus* but included only *P. savii*: Horáček & Hanák (1985*a*, *b*) added *cadornae* and *pulveratus* and suggested the elevation of *Hypsugo* to generic rank, subsequently (1985–1986) widening its possible content and considering it generically distinct.

(*a*) ***savii*** group

Postorbital region, supraorbital region and rostrum not greatly widened; supraorbital tubercles if present small and undeveloped.

(*a*) (i) *pulveratus* subgroup. Braincase elongate, inflated; postorbital region wide, supraorbital area not broadened; rostrum long, not widened; shallow frontal depression; no median rostral depression; broad, shallow lateral depressions above anterior part of orbit; cranial profile somewhat sinuous, depressed over front of orbits; premaxillae not shortened; zygomata robust, with very slight jugal eminence; interdental palate longer than wide; maxillary toothrows almost parallel; moderate bony post-palate; no basal pits; i^2 bicuspid, posterior cusp about 3/4 height of anterior cusp; i^3 large, wide, its crown area equal to or slightly exceeding that of i^2, reaching to tip of the posterior cusp of that tooth, with moderate lateral accessory cusps, lying postero-externally to the inner tooth, separated from c^1 by a moderate diastema; pm^2 about equal or nearly equal to i^3 in crown area, in recess between c^1 and pm^4 which are closely approximated; i_{1-3} slightly imbricated, i_3 a little the largest; pm_2 a little less than 1/2 the crown area of pm_4, 1/2–3/4 its height.

Included taxon: *pulveratus* (Fig. 8c).

(*a*) (ii) *nanus* subgroup. Braincase elevated, slightly inflated, more or less globose but a little elongated; postorbital region wide; supraorbital area slightly widened with small supraorbital swellings; rostrum not especially shortened or broadened; shallow median rostral depression; slight lateral depressions just anterior to supraorbital region; cranial profile sinuous, strongly depressed and concave over rostrum; premaxillae not shortened; zygomata slender, lacking jugal projection; interdental palate longer than wide; maxillary toothrows slightly convergent; short bony post-palate; no basal pits; i^2 unicuspid or with small posterior cusp extending to about 3/4 of its height; i^3 wide, its crown area slightly exceeding that of i^2, about 1/2–3/4 the height of that tooth, extending almost to the tip of its posterior cusp, with slight lateral cusps, lying postero-externally to the inner tooth, separated from c^1 by a wide diastema; pm^2 about 1/2–2/3 or a little more the crown area of i^3, intruded into recess between c^1 and pm^4, these sometimes in contact or nearly so; i_{1-3} not or only very slightly imbricated, i^3 slightly the largest; pm_2 about 1/2 the crown area and height of pm_4.

Included taxa: *arabicus* (Fig. 7a), *culex, helios* (Fig. 6d); probably *musciculus; nanus* (Fig. 6b), *stampflii.*

Current listings (i.e. Hayman & Hill, 1971; Koopman, 1975) unite *helios* with *P. nanus* as a synonym or possibly as a valid subspecies. However, the bacular features of this pale form suggest that it may represent a species distinct from *nanus* with which it may be sympatric in northern and eastern Kenya and in the Sudan. No baculum has been available for *musciculus,* which was placed in a *hesperus* group by Koopman (loc. cit.). Although its incisive and premolar dentition agrees with the *nanus* subgroup its placement here remains speculative.

(*a*) (iii) *savii* subgroup. Braincase rather low and flat, elongate rather than globose; postorbital region not especially widened; supraorbital region unwidened or only slightly widened; rostrum of moderate length; a shallow median rostral depression; usually slight lateral rostral depressions just anterior to supraorbital and anterior orbital rim; cranial profile straight or slightly concave; premaxillae not shortened; zygomata robust, often with slight jugal process; interdental palate a little longer than wide; maxillary toothrows more or less parallel; short bony post-palate; shallow or no basial pits; i^2 unicuspid or with posterior cusp, when present about 3/4 height of anterior cusp; i^3 similar to or exceeding i^2 in crown area, about 1/2–3/4 the height of i^2, with strong central cusp flanked by smaller lateral accessory cusps, lying postero-externally or more laterally (*anchietae*) to the inner tooth, separated from c^1 by a strong diastema; pm^2 much reduced, minute or absent, when present crown area less than 1/2 that of i^3, in recess between c^1 and pm^4, these as a rule in contact; i_{1-3} slightly or more strongly imbricated, similar in size or i_3 slightly the bulkiest; pm_2 reduced, about 1/2 or less in crown area than pm_4 and about 2/3 its height.

Included taxa: *anchietae* (Fig. 6e); probably *ariel*; probably *austenianus*; *bodenheimeri* (Fig. 9f), *caucasicus, darwini, maurus, savii* (Fig. 6a).

We have been unable to examine the baculum of *ariel.* The baculum of a small *Pipistrellus* from the Naturhistorisches Museum, Wien (from Sayala, Upper Egypt) tentatively identified as *ariel* is illustrated by Gaisler *et al.* (1972) but is evidently of the *kuhlii* type. Qumsiyeh (1985) employs the description of this baculum in his account of *ariel.* However, Dr K. Bauer informs us (in litt.) that the specimen (NHW 10351) of which the baculum is figured by Gaisler *et al.* (loc. cit.) is not referable to *ariel* but is instead a small *deserti,* an identification clearly supported by its bacular structure. Moreover, Dr Bauer has loaned three similarly small specimens, one male, the others female (NHW 27501–3) (length of forearm 29·2, 28·9, 28·2; condylobasal length 11·0, 10·5. 10·9; $c–m^3$ 4·0, 3·8, 3·9) apparently from Upper Egypt, that also represent *deserti*: a baculum from this sample is again exactly of the *kuhlii* type. The cranial (narrow braincase, unexpanded rostrum, short broad narial and anterior palatal emarginations, narrow basioccipital) and dental (long i^3, minute pm^2) features of *ariel* clearly indicate that it belongs with *savii,* to which group Koopman (1975) referred it.

A syntype of *Eptesicus bicolor* (Bocage, 1889) (BM(NH) 89.5.1.3) (Fig. 9e) proves to be identical cranially, dentally and in bacular morphology with *Pipistrellus anchietae* (Seabra, 1900) (vide infra, p. 249). However, the point needs confirmation or otherwise by examination of the other syntype in the Museu Nacional de Lisboa. It should be noted that *bicolor* is the prior name (Honacki *et al.,* 1982).

The relationship between the *pulveratus, nanus* and *savii* subgroups is illustrated by *arabicus* and *bodenheimeri,* the bacula of which are compared directly by Harrison (1982). The baculum of *arabicus* (Fig. 7a) approaches that of *anchietae* (Fig. 6e) yet cranially and dentally this species is nearer to *nanus* (Fig. 6b), while that of *bodenheimeri* (Fig. 9f) is like the baculum of *pulveratus* (Fig. 8c) but cranially and dentally the species is close to *savii* (Fig. 6a). These combinations of features link the three subgroups.

(*a*) (iv) *hesperus* subgroup. Baculum a fluted structure, much like that of *pulveratus* or *bodenheimeri*. Braincase low but broad, elongated; postorbital region wide; supraorbital area slightly widened; rostrum short, not greatly broadened; a shallow median frontal depression; slight lateral rostral depressions just above anteorbital foramina; cranial profile almost straight, slightly depressed above anterior root of zygomata; premaxillae not shortened; zygomata slender, a little widened anteriorly, lacking any jugal eminence; interdental palate about as wide as long; maxillary toothrows convergent; short bony post-palate; no basial pits; cochlear bullae inflated with narrow basioccipital; i^2 unicuspid; i^3 slightly greater in crown than i^2 but about 1/2 its height, with little trace of lateral accessory cusps, lying postero-externally, separated from c^1 by moderate to small diastema; pm^2 small to minute, at best about 1/2 or less in crown area than i^3, in recess between c^1 and pm^4 which are closely approximated; i_{1-3} scarcely or not imbricated, similar in size; pm_2 reduced, about 1/2 the crown area of pm_4, a little less than 1/2 its height.

Included taxon: *hesperus* (Fig. 8d).

Horáček & Hanák (1985*a*, *b*, 1985–1986) have indicated that they intend to propose generic status for *hesperus* and indeed have suggested that it be referred to *Parastrellus* which they offer as a new name. It is however a nomen nudum in these publications. There seem good grounds for considering *hesperus* the North American representative of *P.* (*Hypsugo*) to which its bacular, cranial and dental features ally it. Like *bodenheimeri* (Fig. 9f) its baculum approaches that of *pulveratus* (Fig. 8c) but cranially and dentally it is nearer to *savii* and its immediate allies. Koopman (1975) referred *hesperus* to a *hesperus* group in which he also included the African *musciculus*, here provisionally allocated to the *nanus* subgroup.

(*a*) (v) *eisentrauti* subgroup. Braincase broad, elevated and globular; inflated frontally; postorbital region wide; supraorbital region broadened, with small supraorbital tubercles; rostrum short, deep, wide and massive; slight median rostral depression; cranial profile straight or slightly convex; premaxillae not shortened; zygomata strong, lacking any jugal projection; interdental palate very slightly longer than wide; maxillary toothrows almost parallel; short bony post-palate; slight basial pits usually present; i^2 long, narrow, bicuspid, posterior cups about 3/4 height of anterior cusp; i^3 short, wide, similar to or slightly greater in crown area than i^2, about 1/2 or a little more its height, with larger central cusp and smaller lateral accessory cusps, lying laterally and slightly posteriorly to the inner tooth, separated from c^1 by a moderate diastema; pm^2 small, about the same in crown area as i^3, sandwiched into recess between c^1 and pm^4, these almost in contact; i_{1-3} slightly imbricated, i_{2-3} similar in size, both larger than i_1; pm_2 about 1/2 crown area and height of pm_4.

Included taxon: *eisentrauti* (Fig. 9g).

Koopman (1975) places *eisentrauti* in a *rueppellii* group, no doubt on account of its elevated, inflated braincase and its bicuspid i^2, but its bacular features do not associate it with this species and its immediate allies. Its baculum is very similar to that of *imbricatus* (Fig. 9a) or *macrotis* (Fig. 9b).

(*a*) (vi) *imbricatus* subgroup. Braincase inflated, globular, raised posteriorly; postorbital region wide; supraorbital area slightly widened with very small supraorbital tubercles; rostrum short, not especially broadened; no median rostral depression; cranial profile almost straight; slightly concave above supraorbital region; premaxillae not shortened; zygomata moderate to strong, sometimes with a trace of a jugal eminence; interdental palate about as wide as long, not domed; maxillary toothrows almost parallel; very short bony post-palate; well developed basial pits; i^2 bicuspid, posterior cusp about 3/4 height of anterior cusp; i^3 similar in crown area to i^2, about 1/2 its height, with larger central cusp and smaller lateral accessory cusps, lying laterally to the inner tooth, separated from c^1 by a narrow diastema; pm^2 greatly reduced, 1/4 or less the crown area of i^3, in recess between c^1 and pm^4, these in contact; i_{1-3} scarcely imbricated, i_{2-3} of similar size, a little larger than i_1; pm_2 about 1/2 the crown area and height of pm_4.

Included taxa: *curtatus*, *imbricatus* (Fig. 9a), *macrotis* (Fig. 9b), *vordermanni*.

(*a*) (vii) *lophurus* subgroup. Braincase inflated, rounded, slightly elongate, raised posteriorly; postorbital region wide; supraorbital area little widened; at best only a trace of supraorbital tubercles; rostrum moderate in length, longer than in *imbricatus* subgroup, not broadened; no median rostral depression; cranial profile almost straight, slightly depressed or concave above supraorbital region; zygomata strong with distinct jugal eminence; interdental palate a little longer than wide; maxillary toothrows slightly convergent; moderate bony post-palate; deep basial pits; incisor and premolar dentition closely similar to that of *imbricatus* subgroup but i^3 lying more postero-laterally to i^2, and pm^2 sometimes (*lophurus*) slightly larger, about 1/2 crown are of i^3.

Included taxa: *cadornae, kitcheneri* (Fig. 8e), *lophurus* (Fig. 8f).

The baculum of *kitcheneri* is unusual in the presence distally of two anterior dorso-lateral, posteriorly directed processes, with ventrally a more or less tapered median gutter. As in *lophurus*, the tip is directed slightly ventrally.

(*b*) ***stenopterus*** group

Braincase large, rounded and globular; postorbital region very wide; supraorbital region much widened to include well developed supraorbital tubercles; rostrum short, wide; shallow median rostral depression anterior to frontal region; cranial profile slightly convex, elevated over frontal area; premaxillae not shortened; zygomata rather weak, lacking jugal process but usually with small descending process external to m^3; palate short and broad, the interdental palate as wide as long; maxillary toothrows parallel or nearly so; short bony post-palate; shallow basial pits; i^2 small, bicuspid, posterior cusp 1/2–3/4 height of anterior cusp; i^3 a little smaller in crown area than i^2, its tip reaching almost to tip of the posterior cusp of that tooth, with large central cusp and smaller lateral accessory cusps, lying postero-laterally to the inner tooth, only narrowly separated from c^1 or almost in contact with it; c^1 with distinct, well defined posterior accessory cusp; pm^2 small or minute, about equal in crown area or a little larger than i^3 (*stenopterus*) or about 1/3–1/4 the crown area of this tooth (*joffrei, anthonyi*), in recess between c^1 and pm^4, which touch; i_{1-3} not much imbricated, all of similar size; crown area of pm_2 slightly exceeding that of pm_4, pm_2 similar in height to the second tooth (*stenopterus*), or crown area of pm_2 about 1/2 that of pm_4, pm_2 almost as high as that tooth (*joffrei, anthonyi*).

Included taxa: *anthonyi, joffrei, stenopterus* (Fig. 7h).

The baculum of *stenopterus* is unusual, although of the *savii* type: it has a narrow lobed base, hollowed shaft, and expanded tip the lateral margins of which project ventrally as two broadly based 'horns'. The *stenopterus* group as here understood is the *joffrei* group of Tate (1942*a*) and (in part) of Koopman (1973). Both *joffrei* and *stenopterus* have been referred in the past to *Nyctalus* but as mentioned above (p. 234) the baculum of *stenopterus* has no resemblance to the long-shafted baculum of that genus (Fig. 10f). Tate (1942*a*) referred both to *Pipistrellus* with the comment that the group approached Oriental members of the *savii* group, and might at a later time be accorded generic rank.

Subgenus ***Pipistrellus (Falsistrellus)***

Baculum a broad, proximally widened and ventrally deeply fluted structure with no distal expansion; braincase elongate; postorbital region wide; supraorbital area not expanded; rostrum long, not broadened; zygomata moderate to strong; and palate rather narrow, the interdental palate longer than wide.

Pipistrellus (*Falsistrellus*) appears to be related to *P.* (*Hypsugo*) of which it may be the eastern representative. It is approached in bacular morphology by some of the latter subgenus such as *imbricatus* (Fig. 9a), *macrotis* (Fig. 9b), *kitcheneri* (Fig. 8e) and *lophurus* (Fig. 8f), and indeed the baculum in *P.* (*Falsistrellus*) appears to be an extreme variant of the broad, ventrally fluted structure of many of *P.* (*Hypsugo*).

Kitchener *et al.* (1986) raised *Falsistrellus* to generic rank but did not include *affinis* and *petersi*, confining their comparisons to the Australasian *Pipistrellus* (i.e. *adamsi, angulatus, collinus, papuanus, wattsi* and *westralis*) here referred to the *coromandra* subgroup of *P.* (*Pipistrellus*). These authors drew attention to its larger size; to its small i^3 which is anteriorly displaced and swivelled or rotated outwards to lie alongside i^2, its concavity facing outwards (a feature which may have influenced Iredale & Troughton, 1934 in placing it in *Glischropus*); and to its combination of unicuspid i^2, tiny pm^2 and pronounced occipital crest, which as Tate (1942*a*) noted gives the rear of the skull a 'helmeted' appearance. Excepting the large size and the presence of a strong occipital crest, these features occur elsewhere in the various groups of *Pipistrellus*: the extent of the occipital crest may be a function of the large size of the skull.

(a) ***affinis*** group

Braincase rather narrow, mastoid width markedly less than zygomatic width; postorbital region wide; slight, rather poorly developed supraorbital ridges; very shallow median rostral depression just anterior to frontal region; dorso-lateral margin of rostrum more or less straight from postorbital constriction to anterior edge of orbit; cranial profile almost straight, slightly elevated frontally, depressed over supraorbital region; premaxillae not shortened; zygomata moderate to robust with jugal eminence; maxillary toothrows slightly convergent; moderate bony post-palate; no basial pits; i^2 strongly bicuspid, posterior cusp 3/4 or more the height of the anterior cusp; i^3 larger in crown area than i^2, its height about equal to the height of the posterior cusp of that tooth, with strong central cusp and smaller lateral accessory cusps, lying postero-laterally to the inner tooth, separated from c^1 by a moderate diastema; pm^2 almost as great in crown area as i^3 (*affinis*) or about 3/4 its crown area (*petersi*), in recess between c^1 and pm^4; i_{1-3} moderately imbricated, i_3 the largest; pm_2 about 1/2 the crown area of pm_4 and about 2/3–3/4 its height.

Included taxa: *affinis* (Fig. 8a), (?) *mordax, petersi* (Fig. 8b).

It has not been possible to examine *mordax*. Indian records of this species appear to be based on specimens in the collections of the British Museum (Natural History) tentatively labelled as such. These, however, agree closely with the description of *P. affinis* by Dobson (1871) and with the account of a specimen referred to this species from Likiang, Yunnan by Tate (1942*a*). If correctly allocated, *mordax* (Peters, 1867) is the earliest name in the group.

(*b*) ***tasmaniensis*** group

Large and distinctive; braincase high, with well developed sagittal crest; postorbital region wide and strong; no median rostral depression; cranial profile straight; premaxillae slightly shortened; zygomata strong with slight jugal process and small inferior process; maxillary toothrows nearly parallel; short bony post-palate; slight basial depressions; i^2 large, unicuspid; i^3 small, its crown area about 1/4 that of i^2, barely extending above the cingulum of that tooth to which it lies laterally, its hollowed face outwardly directed, separated from c^1 by a moderate diastema: pm^2 very small, about 1/3 the crown area of i^3, in recess between c^1 and pm^4, which touch; i_{1-3} much imbricated, i_3 twice the bulk of i_{1-2}; pm_2 much reduced, about 1/4 the crown area of pm_4 and about 1/2 its height.

Included taxa: *mackenziei* (Fig. 10h), *tasmaniensis* (Fig. 8g)

Subgenus ***Pipistrellus (Neoromicia)***

Baculum with distinct paired basal lobes, slender cylindrical shaft and variously expanded tip; braincase broad, sometimes slightly elongate, rather flattened; postorbital region wide; supraorbital area unwidened or only slightly broadened; rostrum moderate or slightly lengthened; cranial profile straight; premaxillae shortened; zygomata moderate, no jugal process; maxillary toothrows only slightly convergent; short bony post-palate; no basial pits; i^2 unicuspid or with small posterior cusp extending for about 3/4 its height; i^3 smaller than i^2, its crown area 3/4–1/2 or less that of the inner tooth, about 1/2 its height, with usually a larger central cusp and slight lateral accessory cusps, the inner cusp as a rule very small, the tooth anteriorly displaced to lie alongside or almost alongside i^2, separated from c^1 by a moderate to wide diastema; pm^2 almost invariably absent, when present very small, in recess between c^1 and pm^4, i_{1-3} slightly to moderately imbricated, of similar size of with i_{2-3} a little the larger; pm_2 reduced, its crown area 1/2 or less that of pm_4 and its height 1/2–3/4 of the height of that tooth.

This subgenus is wholly African and hitherto its members have been referred to *Eptesicus*, although there is karyological evidence (vide infra) suggesting that one at least should be moved to *Pipistrellus*. It incorporates the *Eptesicus capensis* and *E. tenuipinnis* groups of Koopman (1975).

These can be recognised readily by the structure of the baculum, *capensis* and its allies (Fig. 12a–d, f–i) having the distal part of the baculum spatulate and ventrally deflected, *tenuipinnis* and its associates (Fig. 12e, j) having the baculum modified distally into a lobed, almost vertical plate-like structure.

Published karyological data refers only to *capensis*, although studies of other members of the subgenus are in progress (Rautenbach & Schlitter, 1985*a*, *b*). Peterson & Nagorsen (1975) found that *capensis* has a diploid number of 32 and a fundamental number of 50: Williams & Mares (1978) discussed the possible composite nature of *Eptesicus* as suggested by Koopman (1975) and pointed out that the species fitted karyologically within the variation exhibited by *Pipistrellus*. This genus has a diploid number varying from 26 to 44, and fundamental numbers from 44 to 60, these findings apparently supporting Koopman's observations. These authors remarked, however, that the karyotype of *capensis* is more similar to that of *Pipistrellus nanus* (2N = 36, FN = 50) than to *P. kuhlii* (2N = 44, FN = 50), Koopman having thought *capensis* nearer to the *kuhlii* group than to the *pipistrellus* group in which he placed *nanus*. Williams & Mares (loc. cit.) also found, in contrast, that small *Eptesicus* from the New World (*diminutus*, *furinalis*) have the typical 'eptesicoid' karyotype (2N = 50, FN = 48–50), and added that the karyotypic differences between *Eptesicus* (sensu stricto) and *Pipistrellus* might prove more useful for separating these genera than other structural features.

Our study of the bacula of African *'Eptesicus'* confirms these observations and indicates the isolation of *capensis*, *tenuipinnis* and their relatives from *Eptesicus* sensu stricto (vide infra): Heller & Volleth (1984) also transferred *capensis* to *Pipistrellus*, entirely on account of its published karyology. It is interesting to note also that the baculum of *P. nanus* indicates that this species should be referred to *P.* (*Hypsugo*) rather than to *P.* (*Pipistrellus*) where Koopman (1975) effectively allocated it. The bacular morphology of *capensis*, *tenuipinnis* and their allies suggests strongly that these former groupings of *Eptesicus* are most closely allied to *P.* (*Hypsugo*) as the karyological similarity of *capensis* to *P. nanus* indicates. The anterior upper premolar (pm^2) is very small, vestigial or absent in *P. savii* and is very small in most other members of *P.* (*Hypsugo*): very rarely it is present in *capensis* (Wallin, 1969; Hill & Topál, 1973). On the same point, we have been able to examine a specimen (MJS 2846) from Somalia, in the Carnegie Museum of Natural History, which has a small pm^2 on both sides of the jaw, leading to its erstwhile identification as *Pipistrellus deserti*. The baculum, however, is characteristically that of *'Eptesicus' somalicus*, which in fact the specimen represents.

Koopman (1975) suggested that *Vesperus bicolor* Bocage, 1889 (= *Eptesicus bicolor*) and *Pipistrellus anchietae* (Seabra, 1900), both from Angola, may be conspecific, having examined syntypes of both at the British Museum (Natural History). This author thought that *bicolor* might be a form of *'Eptesicus' tenuipinnis* as Hayman & Hill (1971) suggested, or that it might be based on a specimen of *Pipistrellus anchietae* with missing anterior upper premolars. Bocage (loc. cit.) says 'pas de trace de la premiere premolaire a la machoire superieure'. Further study of the syntype (BM(NH) 89.5.1.3) in London shows it to have a small pm^2 in a recess between c^1 and pm^4 on each side: cranially it agrees exactly with the syntype of *anchietae* (♀ BM(NH) 6.1.3.1) and its baculum is exactly as in that species. Curiously, Bocage states that both original specimens of *bicolor* are female. The specimen in London is quite clearly listed as a 'Co-type' by Thomas in the relevant accession register.

(*a*) ***capensis*** group

Tip of baculum flattened, deflected ventrally, sometimes a small sub-apical dorsal projection; braincase flattened, slightly elongate; rostrum not especially broadened; palate long, narrow, interdental palate longer than wide; i^3 1/2 or less the crown area of i^2.

Included taxa: *capensis* (Fig. 12b, g); probably *brunneus*, *garambae*, *grandidieri*; *guineensis* (Fig. 12c), *matroka* (Fig. 12a), *melckorum* (Fig. 12f); *minutus* (?) (Fig. 12i); probably *rectitragus*; *somalicus* (Fig. 12h); probably *vansoni*; *zuluensis* (Fig. 12d).

The baculum of *brunneus* sensu stricto has not been examined. That (Fig. 14b) of a Nigerian specimen (BM(NH) 48.702) collected by I.T. Sanderson and hitherto referred to this species is very similar to that of *rendalli* (Fig. 12e), with which this example agrees in cranial and ventral characters. The series whence this specimen comes is discussed by Koopman (1965) and Hayman & Hill (1971).

Our study of bacula in this group shows clearly that *matroka* belongs with *capensis*: we have been unable to examine the baculum of *humbloti*. We find too that *capensis* and *somalicus* can be separated by bacular features: the baculum of *capensis* has distally a downwardly directed, plate-like expansion, while in *somalicus* the distal part of the baculum is more spatulate, depressed just below the line of the shaft. Moreover, *zuluensis* is very clearly of the *somalicus* type, and the two appear to be very closely related, as Koopman (1975) suggested. Bacular morphology also confirms the observation by this author that *melckorum* is like a giant *capensis*: Rautenbach & Schlitter (1985*a*, *b*) suggested that these are synonymous.

(*b*) ***tenuipinnis*** group
Tip of baculum expanded into an almost vertical, lobed, plate-like structure; braincase similar to *capensis* group, but broader and less elongate; rostrum slightly widened; palate short and broad, interdental palate about as long as wide; i^3 about 1/2–3/4 the crown area of i^2.

Included taxa: Probably *angolensis, faradjius, flavescens, phasma; rendalli* (Fig. 12e), *tenuipinnis* (Fig. 12j).

Pipistrellus (Arielulus) subgen. nov.

TYPE SPECIES: *Vespertilio circumdatus* Temminck, 1840. Java.

REFERRED SPECIES: *Pipistrellus societatis* Hill, 1972; *Pipistrellus cuprosus* Hill & Francis, 1984.

DISTRIBUTION: Burma to Java (*circumdatus*, Fig. 2e); Malaya (*societatis*, Fig. 9c); Borneo (*cuprosus*, Fig. 9h).

DIAGNOSIS: Differs from most other subgenera of *Pipistrellus* in very small, Y-shaped baculum which has paired basal lobes and a short shaft; baculum similar to that of *P.* (*Perimyotis*) but differing from this subgenus in greatly reduced i^3 and pm^2, the former displaced anteriorly to lie alongside i^2, the latter sometimes absent.

DESCRIPTION: Size small to medium (length of forearm 34·7–43·6); muzzle short, broad and blunt; ears large, rounded, with blunt tip, anterior margin with prominent, posteriorly directed basal lobe, posterior margin with wide quadrate lobe at insertion just behind angle of mouth; tragal margin concave anteriorly, rising to anteriorly directed point, upper margin of tragus nearly horizontal, posterior margin strongly convex; ears and upper margin of tragus edged to a greater or lesser extent with dull white or yellowish white; dorsal pelage black or blackish brown, the hairs tipped with yellowish, orange, russet, copper or bronze.

Braincase high. inflated, globose; postorbital region wide; supraorbital area broadened, with small supraorbital projections or tubercles; rostrum short, widened, sometimes a shallow median rostral depression; cranial profile almost straight, elevated frontally, slightly depressed behind and above supraorbital region; premaxillae not shortened; zygomata strong, no jugal eminence; interdental palate longer than wide; short to moderate bony post-palate; shallow to moderate basial pits; i^2 almost unicuspid, posterior cusp if present insignificant; i^3 very small, about 1/4 the crown area of i^2, 1/3 or less its height, lying almost alongside this tooth, separated from c^1 by a narrow to moderate diastema; pm^2 very small or absent, when present similar in size to i^3, recessed into angle between c^1 and pm^4 which are in contact; i_{1-3} considerably imbricated, i_{1-2} tricuspid or incipiently quadricuspid, i_{2-3} bulkier, larger than i^1, similar in size to each other, their cusps indistinct; pm_2 1/2–1/4 size of pm_4, compressed in toothrow.

ETYMOLOGY: The new subgeneric name is a diminutive of Ariel, a little sprite.

REMARKS: Heller & Volleth (1984) transfer *circumdatus* and *societatis* to *'Eptesicus'* on karyological, bacular and dental grounds. However, the baculum in these species does not resemble closely any of those found either in *Eptesicus* sensu lato or *Eptesicus* sensu stricto. Possibly the unusual baculum in *P.* (*Arielulus*), similar to that of *P.* (*Perimyotis*), is a reduced form of the *P.*

(*Pipistrellus*) type, but the species allocated to *P.* (*Arielulus*) differ widely cranially and dentally from *P. subflavus,* the sole species referred to *P.* (*Perimyotis*).

Genus *Eptesicus* Rafinesque, 1820

Eptesicus Rafinesque, 1820: 2. *Eptesicus melanops* Rafinesque = *Vespertilio fuscus* Palisot de Beauvois.
Cnephaeus Kaup, 1820: 103. *Vespertilio serotinus* Schreber.
Noctula Bonaparte, 1837: fasc. xxi. *Noctula serotina* Bonaparte.
Cateorus Kolenati, 1856: 131. *Vespertilio serotinus* Schreber.
Amblyotus Kolenati, 1858: 252. *Amblyotus atratus* Kolenati = *Vespertilio nilssonii* Keyserling & Blasius.
Pachyomus Gray, 1866: 90. *Scotophilus pachyomus* Tomes.
Nyctiptenus Fitzinger, 1870: 424. *Vespertilio smithii* Wagner = *Vespertilio hottentota* A. Smith.
Rhinopterus Miller, 1906: 85. *Glauconycteris floweri* De Winton. Valid as a subgenus.
Scabrifer Allen, 1908: 46. Substitute for *Rhinopterus* Allen, thought preoccupied by *Rhinoptera* Kuhl, 1841, Pisces.
Pareptesicus Bianchi, 1917: lxxvii. *Vesperugo pachyotis* Dobson.
Rhyneptesicus Bianchi, 1917: lxxvii. *Vesperugo nasutus* Dobson.
Rhineptesicus Horáček & Hanák, 1985–1986: 16. Lapsus.

Baculum more or less triangular, its apex occasionally extended into a short shaft, basally rather wide, sometimes base expanded into small lobes, tip not expanded, usually more or less pointed or gently rounded. There is little flexion in the vertical plane and the tip is not depressed ventrally; transversely the base is sometimes slightly arcuate. Externally and cranially not essentially different from *Pipistrellus* but pm^2 invariably absent, the premolar formula being $\frac{-}{2}\,\frac{-}{-}\,\frac{4}{4}$.

The karyological features of *Eptesicus* are summarised by Heller & Volleth (1984) and Zima & Horáček (1985). Such as have been examined (*andinus, bottae, brasiliensis, diminutus, furinalis, fuscus, guadeloupensis, hottentotus, japonensis, lynni, nilssonii, parvus, serotinus, turcomanus*) are homogeneous in this respect, with 2N = 50, FN = 48–50. On present published knowledge only *capensis* differs with 2N = 32, FN = 50. It is transferred to *Pipistrellus* by Heller & Volleth (loc. cit.) on this account and in the present paper, with others, on bacular grounds. *Pipistrellus societatis* in which 2N is also apparently 50 and FN 48 is transferred to *Eptesicus* by Heller & Volleth (loc. cit.) on account of its karyology and bacular structure, these authors considering it conspecific with *P. circumdatus* (but see Hill & Francis, 1984). Both species are here retained in *Pipistrellus,* with the closely related *P. cuprosus.*

Subgenus *Eptesicus* (*Eptesicus*)

Postorbital region not widened, evident postorbital constriction; rostrum not especially shortened, its dorsal margins not sharply angular; cranial profile straight or slightly concave, not elevated over frontal region; maxillary toothrows almost straight, only slightly convergent; upper surface of forearm, tibia and tail lacking horny excrescences.

(*a*) ***nilssonii*** group

Cranially large, the skull rather elongate; braincase flattened, elongate, no cranial crests; postorbital region slightly widened; supraorbital area unwidened but with very small supraorbital projections; margins of supraorbital region almost straight from postorbital constriction to front of orbit, no prominent supraorbital ridges delimiting upper surface of rostrum; the rostrum long, not widened, rounded dorsally, its upper surface not flattened but transversely convex above; a shallow median rostral depression; slight lateral rostral depressions on each side just above front of orbit; cranial profile straight or almost straight, slightly concave over supraorbital region; premaxillae not shortened; zygomata moderate with slight jugal process; palate long, narrow, interdental palate longer than wide; maxillary toothrows parallel or only slightly convergent; very short bony post-palate; prominent basial pits; tympanic bullae not enlarged, not completely covering cochleae; i^2 bicuspid, posterior cusp about 1/2–3/4 height of anterior cusp; i^3 wide, as large or larger than i^2 in crown area, almost reaching tip of posterior cusp of inner tooth, with very small lateral accessory cusps, not displaced anteriorly, lying postero-laterally to i^2 and separated from c^1 by a moderate diastema; m^3 not greatly reduced, with trace of fourth commissure, the tooth quite long; i_{1-3} slightly imbricated, i_3 a little the largest; pm_2 about 1/2 the crown area and height of pm_4, not compressed in toothrow.

Included taxa: *bobrinskoi* (Fig. 13e), *gobiensis, nilssonii* (Fig. 15a).

If subgeneric recognition is thought justified for this group then *Amblyotus* Kolenati, 1858 is available. The *nilssonii* group was recognised as subgenerically valid by Tate (1942*a*) who however included within it a number of taxa here allocated to the *nasutus* group (vide infra). Strelkov (1986) illustrated the bacula of *nilssonii, bobrinskoi* and *gobiensis,* considering the last to be a valid species.

(*b*) ***nasutus*** group

Cranially small, the skull not especially elongate, braincase flattened, only slightly elongate, broad; postorbital region relatively narrower than in *nilssonii* group; supraorbital area slightly widened; margins of supraorbital region nearly straight from postorbital constriction to front of orbit, supraorbital ridges sometimes prominent; rostrum shortened, its upper margins slightly angular, its upper surface flattened dorso-ventrally, transversely flat, not convex as in *nilssonii* group; a shallow or sometimes more pronounced median rostral depression, slight lateral rostral depressions above front of orbit, small lateral rostral elevations above c^{1-1}; cranial profile straight or nearly so, sometimes slightly concave above supraorbital region; premaxillae sometimes slightly shortened; zygomata moderate, on occasion a slight jugal eminence; interdental palate longer than wide; maxillary toothrows slightly convergent; short bony post-palate; no basial pits; tympanic bullae very large, completely covering cochleae; i^2 large, unicuspid; i^3 small, about 1/2 crown area and height of i^2, with larger main cusp and smaller lateral accessory cusps, anteriorly displaced to lie alongside or almost alongside the inner tooth, separated from c^1 by a moderate diastema; m^3 sometimes reduced, usually with three commissures, no trace of the fourth, antero-posteriorly rather short, compressed, platelet-like; i_{1-3} moderately or well imbricated, similar in size or with i_3 slightly the largest; pm_2 very small, 1/3–1/4 the crown area and 1/2–1/3 the height of that tooth, compressed in toothrow.

Included taxa: *batinensis, matschiei, nasutus* (Fig. 14c), *pellucens, walli.*

Tate (1942*a*) included *walli, matschiei* and *pellucens* in the *nilssonii* group but these agree more appropriately with *nasutus* as De Blase (1980) and Honacki *et al.* (1982) recognised: Ellerman & Morrison-Scott (1951) listed *matschiei* and *pellucens* as subspecies of *nasutus.* Indeed, Tate (loc. cit.) noted the large tympanic bullae of *walli* and the absence of basial pits from this taxon. *Rhyneptesicus* Bianchi, 1917 is available if subgeneric recognition is thought justified for this group.

(*c*) ***serotinus*** group

(*c*) (i) *serotinus* subgroup. Cranially large, the skull elongate; braincase flattened, elongate, often with lambdoid and sagittal crests forming a distinct occipital 'helmet'; postorbital region slightly widened; supraorbital area not widened or only slightly so, with well developed supraorbital ridges in many instances; rostrum long, not broadened, its upper surface flattened but less so than in *nasutus* group; very shallow or shallow median frontal depression, shallow to moderate lateral frontal depressions just above front of orbit; cranial profile almost straight, a slight concavity above front of orbits; premaxillae sometimes a little shortened; zygomata usually robust with moderate jugal projection, on occasion slender to moderate, the projection lacking; palate long and narrow, the interdental palate longer than wide; maxillary toothrows slightly convergent; short bony post-palate; shallow basial pits; tympanic bullae not covering cochleae; i^2 bicuspid, posterior cusp about 3/4 height of anterior cusp; i^3 small to very small, 1/2–1/4 or less the crown area and height of i^2, its tip 1/2 or less the height of the posterior cusp of that tooth, with very small lateral accessory cusps, the tooth displaced anteriorly to lie alongside or almost alongside i^2, separated from c^1 by a moderate to small diastema, sometimes almost in contact with that tooth; m^3 sometimes much reduced, its third commissure obsolescent or obsolete, its second commissure short, the tooth platelet-like; i_{1-3} often massive, much imbricated, i_3 the largest; pm_2 about 1/3–1/2 the crown area and 1/2 the height of pm_4.

Included taxa: *andinus* (Fig. 13d), *argentinus, bottae, brasiliensis* (Fig. 13k), *dorianus, fidelis,* *furinalis* (Fig. 13c), *fuscus* (Fig. 13a), *hingstoni, hispaniolae* (Fig. 13i), *hottentotus, inca, innesi* (Fig. 13j), *innoxius, isabellinus* (Fig. 13h), *megalurus* (Fig. 13b), *melanopterus, montosus, omanensis* (Fig. 14a), *pachyomus, peninsulae, platyops, punicus, serotinus* (Fig. 13g), *shirazensis, sodalis, tatei, turcomanus.*

Tate (1942*a*) has pointed out that the Old World members of this subgroup fall into two categories, one of larger taxa, the other of smaller members of the subgroup. This is also true of the New World taxa: however, here the larger forms are found chiefly in North America, extending only slightly into South America to which the smaller taxa are entirely confined (Thomas, 1920). Material available to us is quite inadequate to attempt any detailed revision and we have followed the lead provided by Tate (loc. cit.) in our allocation of all to the one category. Cranial differences between large and small members of the subgroup appear chiefly to be those associated with size.

The subgroup does not extend substantially into Africa. It is represented in Egypt by *Eptesicus bottae* (*innesi*) and in northwestern Africa by *E. serotinus* (*isabellinus*). Ibáñez & Valverde (1985) consider the West African *platyops* to be a subspecies of *serotinus*, as may be the South African *hottentotus* and also *loveni* from Kenya.

(*c*) (ii) *demissus* subgroup. *Eptesicus demissus* Thomas, 1916 from Thailand appears to be known only from the holotype, which has a damaged skull. It is very similar to the larger members of the *serotinus* subgroup but has a long bony post-palate, prominent basial pits, i^3 about the same in crown area as i^2 and about 1/2 its height, m^3 not especially reduced, its third commissure complete, and with i_{1-3} moderately imbricated, i_3 the largest. We follow Tate (1942*a*) in referring it to a separate subgroup although is likely that more adequate material might enable its status to be determined more precisely.

(*c*) (iii) (?) *pachyotis* subgroup. We have been unable to examine *Eptesicus pachyotis* (Dobson, 1871) from Assam. Little is known of the species, of which the holotype is in the Indian Museum, Calcutta, and as Tate (1942*a*) pointed out, most of the characters given by Dobson in the original description might apply to almost any species of *Eptesicus*. The generic epithet *Pareptesicus* Bianchi, 1917 was proposed for this taxon.

Subgenus ***Eptesicus* (*Rhinopterus*)**

Cranially small; braincase low, flattened and elongate, inflated anteriorly; postorbital region wide; supraorbital area widened with very small supraorbital tubercles; anterior margin of orbit flange-like; rostrum short, flattened dorso-ventrally, its dorsal margins angular; very shallow median rostral depression, shallow lateral depressions just above front of orbit; cranial profile convex, raised above frontal region; premaxillae not shortened; zygomata slender, no jugal projection; palate short, broad, interdental palate about as long as wide; maxillary toothrows convergent; short to moderate bony post-palate; no basial pits; i^2 bicuspid, posterior cusp 3/4 or more the height of the anterior cusp; i^3 small or minute, about 1/4 or less the crown area of i^2, about 1/3–1/2 its height, its lateral accessory cusps very small or obsolete, lying postero-laterally or almost alongside the inner tooth, separated from c^1 by a moderate or small diastema; m^3 not much reduced, its third commissure complete; i_{1-3} strongly imbricated, i_2 the smallest, i_1 and i_3 of similar size; pm_2 very small, about 1/2 crown area and height of pm_4, strongly compressed in row; horny excrescences on upper surface of forearm, tibia and tail.

Included taxa: *floweri* (Fig. 13f), *lowei* (Fig. 13l).

The status of the 'Nycticeini'

An especially interesting feature emerges from our survey of bacular morphology in the Vespertilioninae. The structure of the baculum suggests very strongly that the 'Nycticeini' (or 'Nycticeiini') as presently accepted is not a natural group. Defined chiefly on dental characters (i^2 generally unicuspid, i^3 and pm^2 absent), this group was assembled by Tate (1942*a*) to include *Baeodon, Rhogeessa, Otonycteris, Nycticeius* (i.e. *N. humeralis,* including *cubanus*), *'Scoteinus'* (then including among others the Australian species now referred to *Scoteanax* and *Scotorepens*), *Scotoecus, Scotomanes* and *Scotophilus*. Tate, however, made no mention of the African species *schlieffenii* which was extralimital to his study but which by then had been variously referred either to *Scoteinus* (Miller, 1907) or to *Nycticeius* (Hollister, 1918; Braestrup, 1935). More recently, the type species of *Scoteinus* (the Indian *emarginatus*) has proved to be a *Scotomanes* (Sinha & Chakraborty, 1971) and the other Indian species (*pallidus*) formerly referred to it a *Scotoecus* (Hill, 1974). The Australian *Scoteanax* and *Scotorepens* have been considered to be subgenera of *Nycticeius* (Laurie & Hill, 1954; Koopman, 1978; Corbet & Hill, 1980) but recently have been accorded generic rank (Kitchener & Caputi, 1984; Corbet & Hill, 1986). Thus the current concept of *Nycticeius* is of two species, *N. humeralis* from North America and *N. schlieffenii* from Africa and southwestern Arabia.

The bacula of *Rhogeessa* (Fig. 18k) and *Baeodon* (Fig. 15b) are quite distinctive and are variants of the saddle-like or slipper-like structure found in *Myotis* and *Plecotus* or their allies, as are the very characteristic bacula of *Otonycteris* (Fig. 16a) and *Nycticeius humeralis* (Fig. 17k), the type species of *Nycticeius*. *Scotomanes* (Fig. 18g) and *Scotophilus* (Fig. 17g–j) have bacula reminiscent of the flattened, triangular structure of *Eptesicus* and its immediate associates. In contrast, the bacula of *Scotoecus* (Fig. 20a–e), *Nycticeius schlieffenii* (Fig. 16e), *Scoteanax* (Fig. 16i), and *Scotorepens* (Figs 16g, h, 21e, f) are closely similar to those of *Pipistrellus* (*Pipistrellus*). Thus in bacular terms this supposed group appears to be a composite of different elements, so dissimilar among themselves that its unity seems very unlikely. Kitchener & Caputi (1984) contended on the grounds of a phyletic analysis that *Otonycteris* and *Scotophilus nigrita* fitted poorly into the then current concept of the 'Nycticeini' and moreover on similar considerations that *Nycticeius humeralis* and *Nycticeius schlieffenii* are not congeneric. This view contrasts sharply with that of Koopman (1978) who remarked that the latter are similar in all important characters and should be retained together in the subgenus *Nycticeius* (*Nycticeius*).

The sharp bacular difference between the American *humeralis* and the African *schlieffenii* suggests wider separation and indicates that their congeneric association is wrong, despite their morphological similarities in some other ways. We propose therefore to dissociate *schlieffenii* from *Nycticeius* as generically distinct. The newly proposed genus may be called:

Nycticeinops gen. nov.

Type species: *Nycticejus schlieffenii* Peters, 1860.

Referred species: None.

Distribution: Mauretania to Egypt, Namibia and Mozambique; SW Arabia.

Diagnosis: Baculum (Fig. 16e) distinctive, with expanded base and long fluted shaft, very different from that of *Nycticeius humeralis* (Fig. 17k) which is slipper-like, elevated proximally and distally; cranially similar to *Nycticeius* sensu stricto but rostrum shorter, more narrowed anteriorly, the maxillary toothrows much more convergent, not nearly parallel, with correspondingly narrower narial and anterior palatal emarginations; mandible similarly narrowed anteriorly, with i_{1-3} strongly imbricated, thrust further anteriorly into an arc; narial emargination more clearly U-shaped, not prolonged posteriorly; anterior palatal emargination extending further posteriorly; basial depressions absent or only very slight; pm_2 more reduced. Similar to Australian *Scoteanax* and *Scotorepens* but differing sharply in bacular morphology, the baculum with a more flanged and fluted shaft and lacking the modification of the tip found in these genera, and in less reduction of $m\frac{3}{3}$.

Differs from *Pipistrellus* in massive, unicuspid i^2 which has no trace of a secondary cusp, in contact or nearly so with c^1, the premaxillae greatly shortened, combined with the almost invariable absence of i^3 and pm^2. Similar in some respects to *Scotozous* but differing in bacular morphology; in the presence of a small, posteriorly directed lobe at the base of the inner margin of the ear; tip of tragus anteriorly directed; pm^2 almost invariably absent; pm_2 more reduced. Similar also in some ways to *Scotoecus* but penis not greatly lengthened, baculum similarly shorter, its tip not expanded and bifid; rostrum narrower, uninflated; narial and anterior palatal emarginations not extensively deepened; and anterior face of c^1 rounded, not flattened and grooved.

Description: Small (length of forearm about 29–33 mm); muzzle flattened, anteriorly sparsely haired, nares opening obliquely; ear rounded with broadly rounded tip, anterior or medial margin with small, posteriorly directed basal lobe, anterior margin slightly convex for most of its length; posterior margin nearly straight distally, more convex proximally with well developed, thickened antitragal lobe; tragus with bluntly pointed, anteriorly directed tip, the anterior margin strongly concave basally, straight distally, upper margin nearly horizontal, posterior margin strongly convex, with prominent basal lobe; calcar extending along a little more than one half of the uropatagial border; well developed, rounded post-calacarial lobe or epiblema. Dorsal surface of head and body brown to pale brown, the pelage unicolored; ventral surface paler brown to greyish white, the pelage usually unicolored but in the darker subspecies faintly bicolored, the hair bases darker than the tips.

Skull low, with broad, flattened braincase, not elevated frontally; very low cranial crests and very slight occipital 'helmet'; postorbital region wide; supraorbital area a little broadened; rostrum not expanded laterally, narrow anteriorly; cranial profile almost straight, a little depressed over front of orbits; narial emargination U-shaped, extending posteriorly one half of distance from tip of maxillae to a line joining front of orbits; premaxillae much shortened; anteorbital foramen moderate to large; zygomata slender, no jugal projection; palate rather short, the interdental palate little longer than wide, narrowed anteriorly, maxillary toothrows convergent, anterior palatal emargination narrow, extending posteriorly to a line joining the posterior faces of c^{1-1}, not extending laterally beyond the inner faces of i^{2-2}; short to moderate bony post-palate, a narrow median post-palatal spine; basial depressions at best only very slight.

Dental formula normally $i\frac{-1-}{1\,2\,3}$, $pm\frac{-\,-\,-\,4}{-\,2\,-\,4}$, $m\frac{1\,2\,3}{1\,2\,3}=30$. Upper incisor i^2 massive, unicuspid, usually separated from c^1 by a very short diastema, sometimes in contact with this tooth; i^3 and pm^2 almost invariably absent (Thomas, 1890; Thomas & Wroughton, 1908); pm^4 in contact with c^1, with small protocone; lingual shelves of m^{1-3} widely separated, m^3 not reduced, with three commissures and mesostyle, about 1/2 crown area of m^1 or m^2; i_{1-3} strongly imbricated to one half of their width, thrust forward, i_1 clearly tricuspid, i_{2-3} less obviously so, i_1 longest, i_{2-3} more massive; pm_2 much reduced, 1/2–1/4 crown area of pm_4 and 1/2 its height, compressed in toothrow; m_3 slightly reduced, posterior triangle smaller than anterior triangle, hypoconid and entoconid lower than protoconid, paraconid and metaconid.

Thomas & Wroughton (1908) reported a specimen (BM(NH) 8.4.3.23) from Tette, Malawi in which a well developed i^3 is present in the left side of the jaw. Dobson (1878) remarked of two specimens in the Muséum National d'Histoire Naturelle, Paris that pm^2 is present on one side in one, on both sides in the other, but Thomas (1890) who examined these noted that pm^2 is completely absent from one and present on both sides in the other, Dobson having in the first instance perhaps mistaken a grain of sand for the tooth. Allen (1914) remarked of a specimen that he identified as *schlieffenii* from Bados, Blue Nile Province, Sudan that pm^2 was present on both sides of the jaw and that 'in common with *Scotoecus*, it has a large penial bone, 12 mm long' but Koopman (1965) pointed out that in fact this specimen is a *Scotoecus* (not *Scotophilus* as Qumsiyeh, 1985 avers) and that *schlieffenii* has a very much smaller penis.

Included taxa: The genus is monospecific, its sole species *N. schlieffenii* Peters, 1860. Taxa allocated to it either as valid subspecies or synonyms include *adovanus* Heuglin, 1877; *africanus* Allen, 1911; *albiventer* Thomas & Wroughton, 1908; *australis* Thomas & Wroughton, 1908; *bedouin* Thomas & Wroughton, 1908; *cinnamomeus* Wettstein, 1916; *fitzsimmonsi* Roberts, 1932; *minimus* Noack, 1887.

Etymology: The name of the new genus is derived from νύξ, νυκτόσ or νυκτιοσ, night, and οψ aspect.

Remarks: The type species *schlieffenii* has undergone a wide variety of generic allocations and taxonomic change since Peters (1860) first described it as a *Nycticejus*. Dobson (1876, 1878) placed it in *Scotozous* with *dormeri* while under the impression that this genus lacked i^3, and considered (1878) *Scotozous* to be a subgenus of *Vesperugo*. Noack (1877) and Thomas (1890) referred it to *Scotophilus*, the latter author discussing this genus in relation to *Scotozous*, which following

Dobson he thought to have but one pair of upper incisors. Trouessart (1897) initially followed Dobson (1878) in allocating *schlieffenii* to *Scotozous* as a subgenus of *Vesperugo*, but later (1904) changed this opinion to consider *Scotozous* a subgenus of *Scotophilus*. Miller (1907) referred *schlieffenii* to *Scoteinus*, although in fact the species does not display the reduction of m^3_3 that he considered diagnostic for this genus and which occurs in the Australian species (*balstoni, greyii*, now incorporated into *Scotorepens*) that he allocated to it. Miller's view was adopted by Thomas & Wroughton (1908) and in differing ways by many subsequent authors. However, Allen (1911) when describing *africanus* referred it to the hitherto American genus *Nycticeius*, commenting on its similarity to *N. humeralis* and Hollister (1918) remarked that Old World bats usually placed in the genus *Scoteinus* did not seem to differ generically from the American species of *Nycticeius*, to which he also referred *africanus*. Since then *africanus* has been relegated to subspecific status or synonymy in *schlieffenii* (Braestrup, 1935; Allen, 1939; Aellen, 1952). Braestrup (loc. cit.) also employed *Nycticeius* for *schlieffenii* in preference to *Scoteinus*, and pointed out that its last upper molar was not reduced in the way that Miller (1907) had described for that genus. This author drew attention to the affinity thus established between the Ethiopian and American faunas, but did not exclude the possibility of convergent evolution from different *Pipistrellus*-like forms. Tate (1942*a*) maintained *Nycticeius* and *Scoteinus* as distinct genera but Simpson (1945) united them, a lead followed by many modern authors who have considered *Scoteinus* a subgenus of *Nycticeius*. Thus Ellerman & Morrison-Scott (1951) and Ellerman *et al.* (1953) referred *schlieffeni* to *Scoteinus* as a subgenus of *Nycticeius*, while Laurie & Hill (1954) listed the Australian species before then allocated to *Scoteinus* in *Scoteanax* and *Scotorepens* as further valid subgenera of *Nycticeius*. On the other hand, Rosevear (1965) considered *Nycticeius* and *Scoteinus* synonymous. Koopman (1965) referred *schlieffenii* to *Scoteinus* as a subgenus of *Nycticeius* but later (in litt. in Hayman & Hill, 1971) revised this opinion to allocate it to *Nycticeius* (*Nycticeius*), since then (1978) reinforcing this view.

The classification of the Vespertilioninae

Earlier classifications of the Vespertilioninae (Miller, 1907; Tate, 1942*a*) rely heavily on the pattern of reduction of the incisor and premolar teeth, chiefly on the presence or absence of the outer upper incisor (i^3), of one or both of the first (pm^2) or second (pm^3) upper premolars, and on the presence or absence of the second (pm_3) of the lower premolars, as Tate's 'phyletic' diagrams (loc. cit.) indicate. These dental features have been discussed in more detail above (p. 230): they reflect the degree of shortening that forms an evident trend within the subfamily. When combined with the relative size of one or more of these teeth and the position of the relevant tooth or teeth in the toothrow such factors form an important element in generic identification and diagnosis (cf. Miller, loc. cit.). The many different combinations of incisive and premolar formula in the subfamily (Table 2), the evanescence in some genera of some of the teeth involved, the extreme tendencies towards reduction seen in some such as *Pipistrellus*, and the variety of positions within the toothrow adopted by i^3 and pm^2 in particular reinforce the conclusion that such features reflect a universal trend that may have occurred more than once within the group and which as a result may not provide a totally reliable yardstick by which relationship may be judged.

In addition to these dental features, Tate (1942*a*) reviewed a number of other characters used in the classification of the subfamily. These include the presence or absence of accessory canine cusps; the form and shape of the braincase and rostrum; the degree of reduction of the zygomata; the structure of the palate, its anterior emargination and accessory anterior and posterior spines; the presence or absence of basial pits; enlargement of the ears and their associated bony structures; the presence or absence of adhesive pads on the thumb or foot; and the nature of other minor structures such as the calcar. These features, however, seem of greater value in the distinction of species and species groups, that is, for infrageneric classification, or for the diagnosis of individual genera.

The value of such characters has been discussed at some length by Zima & Horáček (1985) who pointed out that there are grounds for thinking that some of the traditional morphological characters may not provide unequivocally reliable criteria for the establishment of a classification based on presumed phyletic relationship, and that their taxonomic significance may be limited. They also remarked that such characters may reflect parallelism or convergence, or result from selection pressure rather than relationship. These reasons led them to suggest that the baculum might provide one of several alternative sources of reliable, taxonomically useful criteria based on characters that do not have a direct adaptive significance.

The structure of the baculum in the Vespertilioninae suggests some modifications to tribal classification within the subfamily, although clearly other morphological characters need to be given equivalent or greater weight. Provisionally, therefore, we offer an arrangement of the Vespertilioninae in which bacular morphology is used in association with the traditional diagnostic features to suggest possible relationship. This classification is presented in Table 1.

There appear to be two major bacular types in the Vespertilioninae, each with numerous variations as might be expected in such a large and diverse subfamily. A classification that includes a major consideration of bacular morphology shows significant resemblances to earlier arrangements based on traditional and conventional morphological features. However, there are some wide divergences, as for example the seemingly artificial nature of the 'Nycticeini' or the associations of the various genera of big-eared bats. Tate (1942*a*) commented upon the latter and pointed out that very large ears and their associated auditory specialisations in the skull occurred independently in three sections of the subfamily: indeed, if *Antrozous* and *Bauerus* are included, these features occur four times in the group. In particular, both Miller (1907) and Tate (loc. cit.) associated *Laephotis* with *Histiotus* on cranial and dental morphology but its bacular structure shows a clear affinity with *Pipistrellus* (*Neoromicia*) as here recognised. *Otonycteris*, another big-eared bat, was allied by Tate (loc. cit.) to the 'Nycticeini' but proves to have a baculum much more like those of the plecotine genera.

One major bacular type is 'saddle-like' or 'slipper-like' and is exemplified by *Myotis* and *Pizonyx*. Their bacula are very similar, emphasising the close relationship that is generally accepted between these genera. The baculum of *Lasionycteris* is somewhat different in the presence of a lengthened shaft. However, in comparison with the long-shafted bacula found in the Pipistrellini the baculum of *Lasionycteris* is relatively short, and it retains indications of the more characteristic myotine type in its upraised proximal and distal portions. The occasional presence of a flattened dorsal prominence on its base also recalls the condition found in *Idionycteris*. The genus, although having some specialised features, is allied firmly to *Myotis* by Miller (1907) and Tate (1942*a*). It has slightly hooked upper incisors, i^3 with a slightly caniniform profile as in *Myotis*; pm^2 is in the line of the toothrow; m^3 is unreduced; pm_{2-3} are exactly as in *Myotis*, much smaller than pm_4, with pm_3 not removed from the line of the other teeth. Although pm^3 has been lost, this appears to be a specialisation; as Tate (loc. cit.) pointed out, pm_{2-3} still agree closely with those of the less specialised species of *Myotis* not only in relation to each other but also in their proportional size relative to pm_4. Although associated with *Myotis*, this genus is considerably specialised in other ways (Miller, loc. cit.) and its bacular structure may well reflect this divergence. Its baculum might be regarded as derived from the more typical myotine structure.

Bacula variously reminiscent of the saddle shaped structure found in *Myotis* occur in a number of other genera. Such bacula characterise *Plecotus* (including *Coryhorhinus*), *Idionycteris*, *Barbastella*, *Rhogeessa*, *Baeodon*, *Nycticeius*, *Otonycteris*, *Lasiurus*, *Dasypterus*, *Antrozous* and *Bauerus*, and possibly may be found in *Euderma*. Tate (1942*a*) postulated the grouping 'Plecotini' for *Plecotus*, (*Corynorhinus*), *Idionycteris* and *Euderma*, allying it to the Myotini but not employing the term in a formal taxonomic or systematic sense. Bacular morphology thus lends support to his hypothesis that the plecotine genera should be associated with *Myotis*. Also, the baculum of *Barbastella* suggests that it too belongs here: Miller (1907) postulated such a relationship, despite several morphological differences. *Rhogeessa*, *Baeodon*, *Nycticeius* and *Otonycteris* also seem allied to this grouping. Tate (1942*a*) referred these genera to the 'Nycticeini' with *Scotoecus*, *Scotomanes* and *Scotophilus* on account of their incisive and premolar dentition. However, the bacula of *Rhogeessa*, *Baeodon*, *Nycticeius* and *Otonycteris* are variants of the saddle-like type; that of *Scotoecus* is like that of *Pipistrellus* (*Pipistrellus*), and the bacula of *Scotomanes* and *Scotophilus* are broadly similar to those of *Eptesicus* and its allies. *Lasiurus*, *Dasypterus*, *Antrozous* and *Bauerus* have further variants of this bacular type, but are quite distinctive on other morphological grounds.

The bacula of *Antrozous* and *Bauerus* are not at all like that of *Otonycteris*, with which these genera have been tentatively associated (Pine *et al.*, 1971), nor do their bacula have any significant resemblance to those of *Nyctophilus* or *Pharotis*, thus supporting the view (Koopman, 1984*b*, 1985; Breed & Inns, 1985) that these North American genera should not be associated with the Australian *Nyctophilus* and *Pharotis* in the subfamily Nyctophilinae. Bacular morphology suggests instead an association with those genera that have the myotine type of baculum, to which the bacula of *Antrozous* and *Bauerus* have many resemblances. The bacula of *Nyctophilus* and *Pharotis* (Fig. 22a–h) are consistently homogeneous and differ in many ways from those of the genera usually referred to the Vespertilioninae. For the present we would place these two genera in a separate subfamily, the Nyctophilinae, rather than merge them into the Vespertilioninae as is done by Koopman (1984*a*, 1984*b*, 1985).

A further basically triangular and flattened variant of the saddle-like baculum characterises the genera *Eptesicus*, *Vespertilio* (if the pseudobaculum is ignored), *Ia* and *Histiotus*. Miller (1907) remarked that the skull of *Vespertilio* showed a strong likeness to that of *Lasionycteris* but that the former was in all respects a typical *Eptesicus*. *Vespertilio* and *Lasionycteris* are separated by marked dental and bacular differences: the bacular morphology of *Vespertilio* allies it with *Eptesicus* as Miller suggested. It is perhaps not unreasonable to speculate that *Lasionycteris* which has a strongly myotine dentition has diverged among the Myotini in the same way as *Vespertilio* has diverged among the Vespertilionini, the latter genus supporting a long penis either by a centrally situated baculum or perhaps more effectively by the development of a cartilaginous pseudobaculum, this function in *Lasionycteris* by a short shaft. The genera *Tylonycteris* and *Mimetillus* also belong here. The African *Glauconycteris* has been associated (Ryan, 1966; Koopman, 1971) with the Australian *Chalinolobus* but their bacula differ widely. Although structurally variable within the genus, the bacula of *Glauconycteris* are more like the vespertilionine or eptesicine type: those of *Chalinolobus* are long-shafted and like the bacula of *Pipistrellus* (*Pipistrellus*). Finally, the baculum of *Scotomanes* appears to be a derivative of the saddle-like type, leading to the distinctive baculum of *Scotophilus*.

The genus *Pipistrellus* seems to stand more or less at the centre of the second major grouping. It has broadly two divisions in bacular terms, one characterised by a long baculum with well developed basal lobes and a relatively long, mostly cylindrical shaft, its tip often bifid or with similar elaboration. The second division includes those species in which the basal lobes are sometimes small or obsolete and which have a shorter, flatter, ventrally fluted shaft, its tip sometimes elaborated into a spatulate or platelet-like structure.

These groupings have been used in this study to support subgeneric division of this large genus. The first division includes *Pipistrellus* (*Pipistrellus*), *P.* (*Vespadelus*), *P.* (*Perimyotis*) and *P.* (*Arielulus*). Reduction and loss of pm^2 occurs in *P.* (*Arielulus*) and the tooth is almost invariably absent in *P.* (*Vespadelus*). The second division contains *P.* (*Hypsugo*) in which pm^2 may be very small or absent, *P.* (*Neoromicia*) from which it is again almost invariably absent, and *P.* (*Falsistrellus*). Although primarily Old World in distribution, both of these divisions are represented in the New World, each by a single species. The Australian *P.* (*Vespadelus*) seems on bacular features to represent *P.* (*Pipistrellus*); the wholly African *P.* (*Neoromicia*) is apparently similarly related to *P.* (*Hypsugo*), of which *P.* (*Falsistrellus*) appears to be an eastern representative.

The majority of the genera here allocated to the Pipistrellini show strong bacular affinities to *Pipistrellus* (*Pipistrellus*): some such as *Glischropus* and *Scotozous* have been considered congeneric with *Pipistrellus* in the past. Besides *Glischropus* and *Scotozous* these include *Nycticeinops*, *Scoteanax*, *Scotorepens*, *Scotoecus*, *Nyctalus*, *Hesperoptenus* and *Chalinolobus*, all with long-shafted bacula. Of the remainder, *Laephotis* in bacular structure is similar to *P.* (*Neoromicia*), while *Philetor* has a baculum that appears to be an elaboration of the bacular structure found in some of *P.* (*Hypsugo*). Tate (1942*a*) postulated a relationship between *Philetor*, *Tylonycteris* and perhaps *Mimetillus* but the bacula of the first two are totally dissimilar and the structure is apparently absent from *Mimetillus*: it is very small in *Tylonycteris*. Hill (1966*a*) drew attention to the unusual genitalia of *Philetor* and following Tate's (loc. cit.) suggestion of affinity with *Pipistrellus joffrei* and its associates allied *Philetor* with this group. Unfortunately, excepting for the aberrant species *stenopterus* the bacula of the *stenopterus* subgroup (including *P. joffrei*) of this present study remain unknown.

Bacular morphology suggests that the conventional view that *Eptesicus* and its immediate allies derive from or are closely related to *Pipistrellus* can be questioned. Cranially and dentally there are many similarities between *'Eptesicus'* as formerly defined and *Pipistrellus* and as Koopman (1975) has pointed out, the loss of pm^2 enables a species to cross the boundary between the two genera as then understood, a process which in his view might have occurred more than once. Our conclusions do not challenge this opinion: those *'Eptesicus'* species in which pm^2 has been found occasionally to occur prove on bacular grounds to be closer to *Pipistrellus* than to *Eptesicus* as we understand it, while *Pipistrellus* as formerly defined has long been known to include some species from which on occasion this 'diagnostic' tooth is absent. Clearly, our findings support Koopman's (loc. cit.) opinion that this process may have occurred several times and indeed may be occurring in some species, but all belong to the one genus, *Pipistrellus*.

As we understand its composition, *Eptesicus* is now a more restricted genus in which the triangular, flattened baculum is basically closer in structure to the saddle-like grouping than to the long-shafted group, although some *Eptesicus* do indeed have bacula that suggest the beginnings of basal lobulation or of a very short shaft. We suggest therefore that in bacular terms the Vespertilionini to which we refer *Eptesicus* may represent a transitional stage between the saddle-like baculum and the predominantly basally lobed and long-shafted type. *Tylonycteris* and *Glauconycteris* also show this tendency.

Dental reduction proceeds throughout both of the major bacular groups. In the grouping with broadly myotine or saddle-like bacula the dentition varies in number of teeth from a total of 38 (*Myotis, Pizonyx*) through 36 (*Lasionycteris, Plecotus* and allies), 34 (*Barbastella, Eptesicus* and allies), 32 (*Lasiurus*), 30 (*Dasypterus, Rhogeessa, Baeodon, Nycticeius, Otonycteris, Scotomanes, Scotophilus*) to 28 (*Antrozous, Bauerus*). In the second of the two major bacular groups, dental reduction varies from *Eudiscopus* with a total of 36 teeth (its association here is presumed) through 34 (*Pipistrellus, Glischropus, Scotozous, Nyctalus, Chalinolobus*), 32 (*Laephotis, Philetor, Hesperoptenus*) to 30 (*Nycticeinops, Scoteanax, Scotorepens, Scotoecus*). Thus this trend occurs concurrently in the two major groupings, taking the same form in each by increasing the size and bulk of i^2, the reduction, transposition and loss of i^3, and the progressive reduction, transposition and loss of pm^2, pm^3 and pm_2.

Zoogeographical considerations

The saddle-shaped or slipper-like baculum characteristic of the Myotini, Plecotini, Lasiurini and Antrozoini as here understood is cosmopolitan in but one genus, *Myotis*. It occurs in one Holarctic genus, *Plecotus*, in one Palaearctic genus, *Barbastella*, itself probably closely related to *Plecotus*, and in one other Old World genus, *Otonycteris*, that occurs in southwestern Asia and northern Africa. Otherwise this bacular type is limited to the New World. *Lasionycteris*, exclusively North American, has a baculum apparently derived from this type, as does *Nycticeius*, also North American, although in this genus the baculum is considerably modified to the extent that Hamilton (1949) commented upon its unique character among the genera that he had examined. Thus although the saddle-shaped baculum or its derivatives is represented about equally in number of species in the Old and New Worlds, genera with bacula of this type predominate in the latter, its extension into the Old World being primarily through the many species of *Myotis*, with a lesser contribution from *Plecotus, Barbastella*, and *Otonycteris*.

A further variety of this bacular type is found in the Vespertilionini, that is, in *Eptesicus* and its close relatives. In these, the baculum is less strongly saddle-shaped or slipper-like, flatter, and often more triangular in outline. This bacular type is primarily Old World in numbers of genera and species, only *Eptesicus* among Old World genera extending to the New World where there is a closely related genus, *Histiotus*. In the Old World, *Vespertilio* is also closely related to *Eptesicus*. Another Old World genus, *Ia*, is a giant representative of this same bacular type. The southeastern

Asian *Tylonycteris* and the African *Glauconycteris* have bacula that are modified variants of this type: *Mimetillus*, in which no baculum has been found, also appears to belong here. Two further Old World genera, *Scotomanes* and *Scotophilus*, also have bacula that are similar in many respects to the vespertilionine type.

The shafted or long-shafted bacular type is confined almost exclusively to the Old World, and is represented in the New World by no more than two species of *Pipistrellus* in the Nearctic region, one of these with a highly modified baculum. This bacular type is restricted to the Pipistrellini and within that grouping to those genera that for the most part can be shown on other grounds to cluster around *Pipistrellus*. Indeed, some such as *Scotozous*, *Glischropus*, *Scoteanax*, *Scotorepens* and perhaps even *Nyctalus* might on bacular grounds be regarded as subgenera of this widespread genus. In a reduced form this bacular type appears in two of the subgenera of *Pipistrellus*, *P.* (*Perimyotis*) and *P.* (*Arielulus*). Widespread in the Palaearctic region and in southeastern Asia, this bacular type is represented in Australia by five distinct groupings: *Pipistrellus* (*Pipistrellus*), *P.* (*Vespadelus*), *Scoteanax*, *Scotorepens*, and *Chalinolobus*. This type of baculum also occurs in Africa among *Pipistrellus kuhlii* and its associates, which might in fact be considered to warrant recognition as a further subgenus of *Pipistrellus*.

A further variant of the shafted bacular type is found in *Pipistrellus* (*Hypsugo*) and *P.* (*Falsistrellus*). In these the shaft is shorter and is ventrally fluted, often with expansion of the tip. *Pipistrellus* (*Hypsugo*) is confined chiefly to Asia and Africa, where in the latter region it appears to be closely associated with *P.* (*Neoromicia*) in which pm^2 is generally lost. Thus as in Australia where *P.* (*Vespadelus*) in which pm^2 is also generally absent appears to derive from *P.* (*Pipistrellus*), so in Africa *P.* (*Neoromicia*) is apparently similarly related to *P.* (*Hypsugo*). Of the two North American pipistrelles, *P. subflavus* has a reduced form of the *P.* (*Pipistrellus*) baculum, the shaft very short and stubby: this species has a myotine tragus and has been considered (Menu, 1984) to have a myotine dentition. However, on the balance of features it appears to be clearly referable to *Pipistrellus* and indeed to be cranially and dentally close to *P.* (*Pipistrellus*), which apparently it represents in North America. There do not appear to be sufficient grounds to justify its generic separation from *Pipistrellus* as has been recently effected (Menu, loc. cit.), although subgeneric recognition within that genus seems appropriate. The second North American species of *Pipistrellus*, *P. hesperus*, should evidently be referred to *P.* (*Hypsugo*) with which it has close bacular and dental similarities, although recently generic separation (Horáček & Hanák, 1985*a*, *b*, 1985–1986) has been proposed for it. Finally, *P.* (*Falsistrellus*) is restricted to southeastern Asia, Australasia and Tasmania: the deeply ventrally fluted baculum of this subgenus, lacking basal and distal modification but massive and substantial appears to be an extreme of the *P.* (*Hypsugo*) type: possibly *P.* (*Falsistrellus*) represents *P.* (*Hypsugo*) which seems to be linked to it by several of its Asian species.

One corollary of the removal of the African *capensis* and *tenuipinnis* groups of *'Eptesicus'* to *Pipistrellus*, and of the similar transfer of the Australian species formerly referred to *'Eptesicus'* is that in the Old World *Eptesicus* now becomes primarily Palaearctic, with outliers, perhaps all closely connected to *E. serotinus*, in Africa while in the New World it extends over both North and South America. In southeastern Asia the genus becomes restricted to no further east than southern Thailand, the former enormous hiatus in its distribution between this part of southern Asia and Australia having been removed.

Conclusions

(1) The current classification of the Vespertilioninae is based chiefly on adaptive characters with considerable emphasis on facial shortening and concomitant dental reduction and loss. Several authors have drawn attention to the deficiencies and dangers of any classification that relies heavily on such features. A review of bacular morphology within the subfamily suggests that this structure provides indications of relationship that in many respects support the existing classification but which also indicate several changes to the current arrangement. In particular, bacular morphology suggests a number of major and minor changes in the systematics of the nominal genera *Pipistrellus*

and *Eptesicus*, separated hitherto only by dental formula, itself subject to variation in both 'genera' as they are currently understood.

(2) The presence or absence of the anterior upper premolar (pm^2) in *Pipistrellus* and *Eptesicus*, used formerly as their principal diagnostic character, has little taxonomic significance. The tooth is variable in *Pipistrellus* as here understood, being reduced or lost in three of its subgenera, and is absent from *Eptesicus* as we envisage it.

(3) Bacular morphology in *Pipistrellus* and *Eptesicus* provides groupings that largely agree in species content with those proposed by earlier authors such as Tate (1942*a*) and Koopman (1973, 1975) although in basing their studies on 'conventional' morphological characters neither considered these genera in their entirety. The bacular morphology of *'Eptesicus'* as it is currently understood provides a clear indication that as such it is not a natural group, but that three species aggregations, the Australian *pumilus* group and the African *capensis* and *tenuipinnis* groups, should be transferred to *Pipistrellus*.

(4) It has been possible to recognise and define subgenera for the major species groups in both *Pipistrellus* and *Eptesicus* and to suggest possible relationships between them. One subgenus is described as new as *Pipistrellus* (*Arielulus*) for *P. circumdatus* and its allies.

(5) There appear to be clear links between certain of the pipistrelline subgenera: *Pipistrellus* (*Vespadelus*) in Australia seems to represent *P.* (*Pipistrellus*) in bacular terms while *P.* (*Hypsugo*) is apparently represented in Indo-Australia by *P.* (*Falsistrellus*) and is related to the African *P.* (*Neoromicia*). Although the features of the two Nearctic species of *Pipistrellus* have been thought to justify their recognition in separate, individual genera we consider that the characters of one (*subflavus*) merit no more than subgeneric status as the sole species of *P.* (*Perimyotis*), which itself perhaps represents *P.* (*Pipistrellus*), while the other (*hesperus*) is perhaps more appropriately referred to *P.* (*Hypsugo*).

(6) The examination of bacula in *Pipistrellus* has suggested that some taxa hitherto ranked as subspecies, for example *abramus*, *paterculus* or *helios*, might in fact be distinct species.

(7) As we now understand the species content of *Pipistrellus* and *Eptesicus* the former remains primarily an Old World genus where it is widespread and diverse in the tropics and subtropics, extending into the temperate zones and just to North America. In contrast, our concept of *Eptesicus* limits this genus to the New World and in the Old World primarily to the Palaearctic, with outlying representatives in Africa. It does not extend significantly into Australasia.

(8) Bacular morphology suggests the informal recognition of two major groupings within the subfamily Vespertilioninae. The first includes the Myotini, Plecotini and Lasiurini; *Antrozous* and *Baeurus*, which in bacular terms have no relation to *Nyctophilus* and *Pharotis* (the Nyctophilinae); the Scotophilini to include *Scotomanes* and *Scotophilus*; and finally the Vespertilionini, here reduced in content to include *Eptesicus* and its close relatives *Histiotus*, *Ia* and *Vespertilio*, with *Tylonycteris*, *Mimetillus* and *Glauconycteris*.

(9) The second grouping consists of *Pipistrellus* and those genera which cluster round it. All with the possible exception of *Philetor* appear to relate quite closely in bacular terms to one or other of the subgenera that we recognise in *Pipistrellus*, principally to *P.* (*Pipistrellus*). *Laephotis*, formerly considered related to *Histiotus*, is instead in bacular terms closely associated with *P.* (*Neoromicia*). The bacula of *Chalinolobus* and *Glauconycteris* are widely dissimilar athough these genera have been closely allied in the past; *Chalinolobus* is of the pipistrelline type while the baculum of *Glauconycteris* apparently associates it more appropriately with *Eptesicus* and its allies.

(10) Bacular morphology provides clear indications that the 'Nycticeini' of Tate (1942*a*) and Koopman (1984, 1985) is not a natural group, its constituent members despite cranial and dental similarities having widely different bacula. Thus *Rhogeessa*, *Baeodon*, *Nycticeius* sensu stricto, and *Otonycteris* have been here allied to the plecotine bats on bacular grounds, while *Scoteanax*, *Scotorepens* and *Scotoecus* are quite clearly associates in bacular terms of *Pipistrellus*. *'Nycticeius'*, at one time thought to include the Australian *Scoteanax* and *Scotorepens* as well as its North

American type species *humeralis* and the African *schlieffenii*, has recently been restricted only to the American and African forms. These prove to have widely different bacula; *humeralis* has been associated with the plecotine bats on this account, while generic status has been accorded to *schlieffenii* with the proposal of a new generic name, *Nycticeinops*.

(11) The two broad bacular types that we discern in the subfamily Vespertilioninae have definite geographical patterns: the saddle-like baculum and its variants that characterise the first group noted above is primarily New World and Palaearctic, extending less significantly into the Old World tropics or Australasia, while the shafted baculum of the second group is chiefly confined to the Old World.

Addendum

A phenetic analysis of the relationships of selected vespertilionine species (chiefly those currently referred to *Pipistrellus* and *Eptesicus*) by Horáček & Hanák (1985–1986) appeared while this paper was in press. These authors provided definitions of *Pipistrellus, Hypsugo* (which they considered generically valid) and *Eptesicus*, based on the morphology of the penis and baculum, the upper molars, the basisphenoid pits, the pelvic girdle, and the tibia, tail and epiblema.

Horáček & Hanák suggested that the classification of pipistrelloid bats might be clarified by the recognition of additional subgenera or genera for those species or species groups that do not conform precisely with those that they included within these three generic groupings. To some extent such recognition is provided in several instances by the classification here proposed and although some major differences exist between the informal assessments and species groups of Horáček & Hanák and the formal arrangement put forward in this paper there is nevertheless a broad measure of agreement. Horáček & Hanák did not attempt any classification of the Vespertilioninae as a whole, but '*Nycticeius*' *schlieffenii*, here considered to represent a distinct monospecific genus (*Nycticeinops* gen. nov.) was thought by these authors to be referable either to *Eptesicus (Rhyneptesicus)*, or possibly to justify the establishment of a new subgenus within *Eptesicus*.

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Appendix 1. Specimens examined

AMNH = American Museum of Natural History, New York
BM(NH) = British Museum (Natural History), London
CMNH = Carnegie Museum of Natural History, Pittsburgh
HZM = Harrison Zoological Museum, Sevenoaks, Kent
NMW = Naturhistorisches Museum, Wien

Vespertilioninae

Myotis nattereri
HZM 26.11254 Leany Cave, Pilis Heights, Hungary. (Fig. 19j)

Myotis ridleyi
BM(NH) 98.3.13.5 Selangor, Malaya. Holotype. (Fig. 19i)

Pizonyx vivesi
HZM 3.10284 Isla Cordonosa, Bahia de Los Angeles, Baja Norte, Mexico. (Fig. 19k)

Lasionycteris noctivagans
BM(NH) 7.7.7.2319 Raleigh, North Carolina, USA. (Fig. 17f)
HZM 2.3708 Delta, Manitoba, Canada

Plecotus auritus
HZM 19.1227 Near Godstone, Surrey, England. (Fig. 19g)

Plecotus austriacus
BM(NH) 91.10.5.4 Duirat, Tunis
HZM 3.4867 St. Pierre de Varenne, Saone et Loire, France.
HZM 4.8337 Mont de Lans, Les Deux Alpes, Isere, France.
HZM 5.8467 Chateau de Salse, Salse, Rousillon, France. (Fig. 19h)

Barbastella barbastellus
HZM 13.11222 Kiralyret, Borzsony Heights, Hungary. (Fig. 18j)

Rhogeessa tumida
HZM 1.12080 Airport Camp, Belize. (Fig. 18k)

Nycticeius humeralis
AMNH 249144 Sierra de Tamaulipas, Acuna, Tamaulipas, Mexico, 2890 ft. (Fig. 17k)

Otonycteris hemprichii
BM(NH) 14.8.17.1 Syrian Desert.
HZM 6.8174 17 km N of Hufoof, Saudi Arabia. (Fig. 16a)

Lasiurus cinereus
HZM 1.3695 S Fork, Cave Creek, near Portal, Cochise County, Arizona, USA. (Fig. 19l)

Dasypterus argentinus
BM(NH) 33.6.24.3 Bonifacio, Argentina. (Fig. 18f)

Antrozous pallidus
BM(NH) 50.767 California, USA. (Fig. 18b).
HZM 3.3692 S Fork, Cave Creek, near Portal, Cochise County, Arizona, USA.

Scotophilus borbonicus
BM(NH) 89.1.11.2 E coast of Africa.

Scotophilus dinganii
BM(NH) 79.513 Tokadeh, Nimba, Liberia, 600 m.

Scotophilus heathii
BM(NH) 14.7.19.19 Mount Popa, Burma.
BM(NH) 14.7.19.28 Kyauk Inyaung, Irrawaddy, Burma.
BM(NH) 60.257 Tori, Pakistan. (Fig.17h)
BM(NH) 70.1488 Bang Phra, Cholburi, Sriracha, Thailand.
BM(NH) 76.787–788 Nhatrang, Annam, Vietnam.

Scotophilus kuhlii
BM(NH) 75.2955 Chiang Mai, Thailand (Fig. 17i)

Scotophilus nigrita (gigas)
BM(NH) 22.12.17.55a Mtondo, Ruo, Malawi. (Fig. 17g)

Scotophilus nigritellus
BM(NH) 78.189 Numan, Gongola, Nigeria. (Fig. 17j)

Scotomanes ornatus
BM(NH) 94.9.1.21 Foochow, China. (Fig. 18g)

Eptesicus (*Eptesicus*)

Eptesicus bobrinskoi
BM(NH) 63.1187 Guter Su, N of Mount Sabalan, NW Iran. (Fig. 13e)

Eptesicus nasutus
HZM 3.4571 Harmul, 10 m N of Sohar, Oman (*batinensis*).
HZM 12.11172 Jamma, near Rostaq, Oman (*batinensis*). (Fig. 14c)
HZM 1.1623 Shaiaba, Iraq (*pellucens*).

Eptesicus bottae
HZM 18.1616 Ser'Amadia, Kurdistan, Iraq.
HZM 5.1628 Basrah, Iraq (*hingstoni*).
BM(NH) 3.12.8.9 Cairo, Egypt (*inncsi*). (Fig. 13j)
HZM 12.8075 Birkat Sharaf al Wadi Sahtan, Jebel al Akhdar, Oman (*omanensis*). (Fig. 14a)

Eptesicus brasiliensis
BM(NH) 85.6.26.10 San Lorenzo, Rio Grande do Sul, Brazil. (Fig. 13k)
BM(NH) 0.6.29.4 Palmeira, Parana, Brazil.
BM(NH) 98.10.3.32 Valdivia, Colombia (*andinus*). (Fig. 13d)

Eptesicus furinalis
BM(NH) 4.8.8.5 La Plata, Argentina. (Fig. 13c)

Eptesicus fuscus
BM(NH) 89.6.1.4 Sing Sing, New York, USA. (Fig. 13a)
BM(NH) 52.551 Chinchona, Jamaica (*hispaniolae*). (Fig. 13i)

Eptesicus hottentotus
BM(NH) 81.7.11.1 Drakenburg Mountains, Natal, South Africa (*megalurus*). (Fig. 13b)

Eptesicus serotinus
BM(NH) 53.555 Blandford, Dorset, England. (Fig. 13g)
HZM 3.629 Shepreth, Cambridgeshire, England.
BM(NH) 66.1150 Defilia Oasis, Figuig, Morocco (*isabellinus*). (Fig. 13h)

Eptesicus (*Rhinopterus*)

Eptesicus floweri
BM(NH) 0.8.6.20 Abu Zeit, White Nile, Sudan. (Fig. 13f)
BM(NH) 1.5.5.78 Shendy, Sudan (*lowei*). (Fig. 13l)

Vespertilio orientalis
BM(NH) 8.7.25.6, BM(NH) 8.8.11.2 Kuatun, NW Fokien, China

Histiotus macrotis
BM(NH) 71.1123 Antofagasta, Lake Miniques, Chile, 1450 m. (Fig. 18e)

Histiotus (?) *macrotis*
BM(NH) 6.5.8.3 Jafi, Tucuman Province, Argentina. (Fig. 18d)

Histiotus velatus
BM(NH) 0.6.29.2 Palmeira, Parana, Brazil. (Fig. 18c)

Tylonycteris pachypus
BM(NH) 9.1.5.954 Buitenzorg, Java. (Fig. 18h)

Tylonycteris robustula
BM(NH) 60.1499 Bukit Lagong Forest Reserve, Kepong, Selangor, Malaya. (Fig. 18i)
HZM 3.7444 15th mile Ulu Gombok, Selangor, Malaya.

Mimetillus moloneyi
BM(NH) 93.1.7.2 Leekie, Nigeria
BM(NH) 54.862 Irumu, Zaire.
BM(NH) 60.154 Bo, Sierra Leone.
BM(NH) 64.1788 Liwale, Tanzania.
HZM 2.7802 Near Babeke, River Isai, Ituri, Zaire.

Glauconycteris argentata
BM(NH) 54.863 Banana, Zaire.
BM(NH) 59.510 Ikela, Ikela Territory, Zaire. (Fig. 19d)

Glauconycteris beatrix
BM(NH) 48.713 Eshobe, Mamfe, Cameroun. (Fig. 19c)

Glauconycteris humeralis
BM(NH) 30.11.11.173 River Wasa, Semliki Valley, Uganda. (Fig. 19e)

Glauconycteris poensis
BM(NH) 96.12.31.2 Sierra Leone.
BM(NH) 69.26 Abidjan, Ivory Coast. (Fig. 19a)

Glauconycteris variegata
BM(NH) 76.780 Mole National Park, Ghana. (Fig. 19b)
BM(NH) 55.409 Mongue, near Inhambane, Mozambique (*papilio*). (Fig. 19f)

Pipistrellus (Pipistrellus)

Pipistrellus pipistrellus
HZM 94.6807 Rabat, Malta.
HZM 116.8549 Sevenoaks, Kent, England. (Fig. 2a)
HZM 117.8650 Aylesford, Kent, England.
BM(NH) 73.689 Kululai Rest House, Northwest Frontier Province, Pakistan (*bactrianus*)
BM(NH) 14.5.10.19 BM(NH) 14.5.10.22 Djarkent, Semiretschenskoi, USSR (*lacteus*).

Pipistrellus nathusii
BM(NH) 8.8.4.128 BM(NH) 62.1368 St Giles, France (Fig. 2b)

Pipistrellus abramus
BM(NH) 89.6.17.3–4 Kin Kiang, Yangtse Kiang, China (seen by Thomas, 1928*a*).
BM(NH) 5.1.4.8 Tokyo, Japan.
BM(NH) 7.7.3.26 Nanking, China (seen by Thomas, 1928*a*). (Fig. 3a)
BM(NH) 14.10.1.1 Lokow, Hunan, C China.
BM(NH) 26.10.4.18 Hue, Annam, Vietnam (seen by Thomas, 1928*a*)
BM(NH) 66.3469–3470 Chihli, China.
BM(NH) 86.529 Chusan, China (Syntype *irretitus*).
BM(NH) 86.532 Canton, S China.

Pipistrellus babu
BM(NH) 45.1.8.403 Nepal.
BM(NH) 16.3.25.8 Pashok, Darjeeling, India. (Fig. 4a)

Pipistrellus camortae
BM(NH) ——— Car Nicobar (Original No. 3/76). (Fig. 15d)

Pipistrellus endoi
BM(NH) 70.2522 Horobe, Tayama, Ajiro-Machi, Minohe-Gun, Iwate Prefecture, Japan. (Fig. 3b)

Pipistrellus javanicus (*tralatitius*)
BM(NH) 0.8.2.9 Sumatra.
BM(NH) 9.1.5.295 Tjilatjap, Java.
BM(NH) 9.1.5.997–998 W Java.
BM(NH) 16.4.21.3 Sungei Penoh, Korinchi, Sumatra.

BM(NH) 27.12.1.37 Tam Dao, Tonkin, Vietnam, 3000 ft (No. 411 of Thomas, 1928*a*).
BM(NH) 28.7.1.20 Phu Qui, Annam, Vietnam, 100 ft (No. 866 of Thomas, 1928*b*, who identified the specimen as *P. coromandra tramatus*, but with a longer baculum than those previously examined).
BM(NH) 83.76 Silau Silau Trail, Mount Kinabalu, Sabah, Borneo. (Fig. 10e)

Pipistrellus paterculus
BM(NH) 14.7.8.62 Pyaunggaung, N Shan States, Burma, 2794 ft.
BM(NH) 14.7.19.241 Kyauk Myaung, Irrawaddy, W Burma.
BM(NH) 14.7.19.242 Mount Popa, Upper Burma (Holotype). (Fig. 3c)
BM(NH) 14.7.19.240 Mandalay, Burma.

Pipistrellus angulatus
BM(NH) 67.2125 Schoolmaster's House, Nuhu, Guadalcanal I, Solomon Is (*ponceleti*). (Fig. 4d)

Pipistrellus collinus
BM(NH) 50.983 Baiyanka, Purari-Ramu Divide, SE Bismarck Range, Papua New Guinea. (Fig. 4b)

Pipistrellus coromandra
BM(NH) 32.11.1.7 Nam Tamai, Upper Burma.
BM(NH) 50.478 Ningma, Upper Burma.
BM(NH) 76.1263 Sumka Uma, Upper Burma.
HZM 1.7317, HZM 2.7318 Near Mirzapur, India. (Fig. 7c, HZM 2.7318)
HZM 4.7320 Dalatpur, near Mirzapur, India.
BM(NH) 4.6.8.1 Annam, Vietnam (*tramatus*). (Fig. 7b)
BM(NH) 27.12.1.40 Bac-kan, Tonkin, Vietnam (*tramatus*) (Original No. 444, seen by Thomas, 1928*a*).

Pipistrellus mimus
BM(NH) 98.5.5.20 Dangs, Bombay, India.
HZM 1.10456 Vikas Vidyalaya, near Ranchi, Bihar, India. (Fig. 7g)

Pipistrellus murrayi
BM(NH) 99.8.6.34 Christmas I, Indian Ocean (Holotype). (Fig. 4c)
BM(NH) 9.1.16.7 Flying Fish Cove, Christmas I, Indian Ocean.

Pipistrellus papuanus
BM(NH) 22.2.2.3 Fredrik Hendrik I, Irian Jaya. (Fig. 2c)
BM(NH) 34.1.14.8 Kokoda, Papua New Guinea.

Pipistrellus tenuis
BM(NH) 85.912 Coast of Sabah, Borneo (*nitidus*). (Fig. 9d)

Pipistrellus ceylonicus
BM(NH) 95.6.12.1 Pundibiya, India.
BM(NH) 2.4.2.8 Astoli, Belgoum, India. (Fig. 7d)
BM(NH) 11.4.5.5 Lanje, Konkan, India.
BM(NH) 13.9.8.102 Gujerat, India.
BM(NH) 9.1.4.73 Mangalore, Malabar Coast, India (Holotype *indicus*)
BM(NH) 4.6.8.7–8 Tonkin, Vietnam (*raptor*). (Fig. 3d, BM(NH) 4.6.8.7 Holotype).

Pipistrellus crassulus
BM(NH) 4.2.8.1 Efulen, Cameroun (Holotype). (Fig. 7e)

Pipistrellus nanulus
BM(NH) 4.2.8.8 Efulen, Cameroun (Holotype). (Fig. 7f)
BM(NH) 79.508 South Nimba, Liberia.

Pipistrellus rueppellii
BM(NH) 68.12.22.3 Zanzibar (Holotype *pulcher*). (Fig. 10a)
BM(NH) 99.9.9.20 Egypt.
BM(NH) ——— Uganda. (Fig. 10b)
HZM 3.3170 Kabompo Boma, Zambia.
HZM 7.12109 Suez, Egypt.

Pipistrellus deserti
BM(NH) 79.987 Hoggar Plateau, Algeria. (Fig. 5c)
NMW 27503 (?) Upper Egypt.

Pipistrellus kuhlii
BM(NH) 92.9.9.25 Upper Egypt.
BM(NH) Argostoli, Cephaloni, Greece. (Fig. 5a)
BM(NH) 63.335 Sangha, Malya Khola, E Nepal.
HZM 5.11607 Horefto, near Volos, Greece.
HZM 11.1016 Rapallo, N Italy.
HZM 138.4563 Yal bu Hillal, Batinah, Oman.
HZM 154.4619 Saham, Batinah, Oman.
HZM 203.7232 Dig Dagga, Ras al Khaima, United Arab Republic.
HZM 218.7402 Benghazi, Libya.
HZM 227.9110 Kapsowat, Marakwat, Kenya.

Pipistrellus maderensis
BM(NH) 86.528 Madeira. (Fig. 5b)

Pipistrellus rusticus
BM(NH) 35.9.1.108 Okavango-Omatako Junction, Grootfontein District, Namibia.
BM(NH) 79.1731 Oli River, Borgu G.R., Nigeria. (Fig. 6c)
HZM 4.3285 Sentinel Ranch, River Limpopo, Zimbabwe. (Fig. 5d)

Pipistrellus (*Vespadelus*)

Pipistrellus pumilus
BM(NH) 70.1093 E Bonithon Range, C Australia 23°42′S, 129°02′E, 1400 ft.
BM(NH) 71.1497 Westwood, near Rockhampton, Queensland, Australia. (Fig. 12k)

Pipistrellus (*Perimyotis*)

Pipistrellus subflavus
HZM 1.2422 Big Wyandotte Cave, Crawford County, Indiana, USA. (Fig. 2d)

Pipistrellus (*Hypsugo*)

Pipistrellus anchietae
BM(NH) 69.1248 Ngoma, Zambia.
BM(NH) 70.2632 Balovale, Zambia. (Fig. 6e)
BM(NH) 89.5.1.5 Caconda, Angola (Syntype of *Vesperus bicolor* Bocage, 1889). (Fig. 9e)

Pipistrellus bodenheimeri
HZM 3.3786 Jazirat al Abid, Aden, South Yemen.
HZM 5.8279 Ein Gedi, Israel. (Fig. 9f)

Pipistrellus savii
BM(NH) 31.11.11.13, BM(NH) 66.4644 E slope of Mount Olympus, Greece.
BM(NH) 61.395 Ainab, Lebanon. (Fig. 6a)

Pipistrellus arabicus
HZM 4.10060 Wadi Sahtan, Oman.
HZM 5.11625 Wadi Fidah, Dank/Ibri, Oman. (Fig. 7a)

Pipistrellus helios
BM(NH) 39.133 N Guaso Nyiro, Kenya. (Fig. 6d)
BM(NH) 69.207 Kangatet, S Turkana, Kenya.
HZM 2.4086 Archer's Post, Northern Frontier District, Kenya.

Pipistrellus nanus
BM(NH) 49.484 Kontaur, Gambia.
HZM 3.2778 Sokoto, N Nigeria.
HZM 3.4026, HZM 4.4027 Near Monrovia, Liberia.
HZM 83.4387 Haroni-Lusitu Beacon 74, Zimbabwe.
HZM 107.3212 Kabompo Boma, Zambia.
HZM 146.5161, HZM 147.5162 Rondo, Lindi, Tanzania.
HZM 165.5321 Liwale, Tanzania.
HZM 200.6581 Karonga, Malawi.
HZM 258.11469 Kunyale Stream, Mwinilunga District, Zambia.

HZM 260.12175 Lamto, Ivory Coast.
HZM 261.12176 Ivory Coast.
HZM 263.12451, HZM 264.12452 Kamuani Area, Machakos District, Kenya. (Fig. 6b, HZM 263.12451)

Pipistrellus pulveratus
BM(NH) 79.702 Near Nicholson Goat Bungalows, Hong Kong I.
BM(NH) 79.903 Peace Mansion, Tai Hang Road, New Territories, Hong Kong (Fig. 8c)

Pipistrellus hesperus
BM(NH) 98.3.1.8 Sierra Laguna, Baja California, Mexico.
BM(NH) 29.11.7.10 Panamint Mts, California, USA.
HZM 4.11219 Sycamore Well, Hidalgo County, New Mexico, USA. (Fig. 8d)

Pipistrellus eisentrauti
BM(NH) 84.1684, BM(NH) 84.1686 Mount Cameroun, Cameroun. (Fig. 9g, BM(NH) 84.1684)

Pipistrellus imbricatus
BM(NH) 9.1.5.286 Buitenzorg, Java. (Fig. 9a)

Pipistrellus macrotis
BM(NH) 23.1.2.12 Sabang, NW Sumatra. (Fig. 9b)

Pipistrellus kitcheneri
BM(NH) 10.4.5.47 Boentok, Barito River, Kalimantan, SC Borneo. (Fig. 8e)

Pipistrellus lophurus
BM(NH) 14.12.1.6 Maliwun, Victoria Province, Tenasserim, Burma (Holotype). (Fig. 8f)

Pipistrellus stenopterus
BM(NH) 60.1537 Institute of Medical Research Compound, Kuala Lumpur, Malaya.
BM(NH) 65.135 Pasir Road, Kuala Lumpur, Malaya. (Fig. 7h)

Pipistrellus (*Falsistrellus*)

Pipistrellus affinis
BM(NH) 83.3.3.2 Wynaard, India. (Fig. 8a)
BM(NH) 72.4224 Argarawa, Nevrawa Elwa, Central Province, Sri Lanka.

Pipistrellus petersi
BM(NH) 23.1.2.3. Buru I, Molucca Is (Fig. 8b)

Pipistrellus tasmaniensis
HZM 1.8712 Barrington Tops National Park, New South Wales, Australia. (Fig. 8g)

Pipistrellus (*Neoromicia*)

Pipistrellus capensis
BM(NH) 32.9.1.249 Broken Hill, Zambia.
BM(NH) 54.859 Elizabethville, Zaire.
BM(NH) 61.1078 Doddieburn Ranch, West Nicholson, Zimbabwe, 2300 ft, 21°24′S, 29°21′E.
BM(NH) 72.4383 E of Lake Margharita, Bulcha Forest, Ethiopia, 1800 m, 06°11′N, 36°10′E.
BM(NH) 72.4391 Didessa River, Wollega Province, Ethiopia, 1190 m, 09°02′N, 36°09′E. (Fig. 12g)
BM(NH) 75.561 Mole National Park, Ghana. (Fig. 12b)
BM(NH) 83.200 Mcheni Gorge, Chizarira National Park, Binga Province, Zimbabwe, 17°40′S, 27°52′E.
HZM 36.4514 40 m NW of Serowe, Botswana.
BM(NH) 66.6057 Ambositra, Madagascar (*matroka*). (Fig. 12a)
BM(NH) 77.2.19.6 Anzahameru, Madagascar (*'minutus'*). (Fig. 12i)

Pipistrellus guineensis
BM(NH) 70.2224, BM(NH) 70.2228, BM(NH) 72.4373 Gambela, Ethiopia, 8°15′N, 34°35′E (BM(NH) 72.4373 at 515 m) (Fig. 12c, BM(NH) 70.2224)
BM(NH) 76.293 Shagamu, Nigeria.
BM(NH) 84.1019 Bontioli, Bougouriba River, Burkina Faso (Upper Volta).

Pipistrellus melckorum
BM(NH) 83.216 Mcheni Gorge, Chizarira National Park, Binga Province, Zimbabwe, 17°40′S, 27°52′E. (Fig. 12f)

Pipistrellus somalicus
BM(NH) 70.484 Mouth of Fincha River, Blue Nile Gorge, Ethiopia, 10°03′N, 37°20′E. (Fig. 12h)
BM(NH) 76.814 S bank of Ganale Doria, Sidam-Bale Bridge, Sidamo Province, Ethiopia, 5°45′N, 39°37′E.
BM(NH) 84.1016 Comoe River, Burkina Faso (Upper Volta), 260 m, 9°57′N, 4°38′W.
CMNH MJS 2846 Snai Sugar Plantation, 1½ km S, ½ km E of Giohar, Somalia, 2°46′N, 45°31′E.

Pipistrellus zuluensis
BM(NH) 83.212 Mchesu River, Chizarira National Park, Binga Province, Zimbabwe, 17°47′S, 27°39′E.
BM(NH) 83.215 Singama, Sibuwa, Binga Province, Zimbabwe, 17°36′S, 27°51′E. (Fig. 12d)

Pipistrellus rendalli
BM(NH) 89.12.12.1 Bathurst, Gambia.
BM(NH) 7.12.17.1–2 Gondokoro, White Nile, Sudan.
BM(NH) 23.4.12.1–2 Bugala, Sesse Is, Victoria Nyanza, Uganda. (Fig. 12e, BM(NH) 23.4.12.2)
BM(NH) 48.702 N'ko, Obubra Division, S Nigeria (?*brunneus*). (Fig. 14b)

Pipistrellus tenuipinnis
BM(NH) 47.350 Umuahia, E Nigeria.
BM(NH) 54.917 Bonthe, Sierra Leone.
BM(NH) 67.1734 Bota, Victoria, Cameroun, 4°00′N, 9°05′E. (Fig. 12j)

Pipistrellus (*Arielulus*)

Pipistrellus circumdatus
BM(NH) 73.618 Telecommunications Tower, Fraser's Hill, Pahang, Malaya. (Fig. 2e)

Pipistrellus cuprosus
BM(NH) 83.351 Sepilok, Sabah, Borneo, 5°52′N, 117°56′E (Holotype). (Fig. 9h)

Pipistrellus societatis
BM(NH) 67.1605 Base Camp, Gunong Benom, Pahang, Malaya, 800 ft (Holotype). (Fig. 9c)

Nyctalus noctula
BM(NH) ——— Locality unknown.
HZM 10.613 Bottisham, Cambridgeshire, England.
HZM 33.8888 Winchelsea Beach, Sussex, England. (Fig. 10f)

Laephotis botswanae
BM(NH) ——— Zomba, Malawi (original No. 2269; damaged).

Laephotis wintoni
HZM 1.3020 Nyeri, Mount Kenya, Kenya. (Fig. 16f)

Glischropus tylopus
BM(NH) 10.4.5.136 Upper Barito River, Kalimantan, SC Borneo. (Fig. 18a)

Scotozous dormeri
BM(NH) 12.3.8.30 Furdapur, Ajanta, Khandesh, India.
BM(NH) ——— Kathiawar, India (Original No. BNHS 2007). (Fig. 16d)

Scoteanax rueppellii
BM(NH) 80.3.25.1 Richmond River, New South Wales, Australia. (Fig. 16i)

Scotorepens balstoni
BM(NH) 10.6.21.9 Hermannsburg, Northern Territory, Australia. (Fig. 16g)

Scotorepens greyii
BM(NH) 75.2261 Pine Creek, 20 m ESE of Gandy's Hill, Northern Territory, Australia, 13°49′S, 131°49′E. (Fig. 16h)

Nycticeinops schlieffenii
BM(NH) 14.7.31.14 Wei Wei River, Kenya.
BM(NH) 15.3.6.66 Kamisu, Dinda River, Sudan.
BM(NH) 71.675 Awash, Filhoa, Ethiopia, 09°00′N, 38°58′E.
HZM 5.2120 Ikau, Rukwa, Tanzania. (Fig. 16e)

Scotoecus albigula
BM(NH) 63.1042 Calundo, Lunda, Angola. (Fig. 20a)

Scotoecus albofuscus
BM(NH) 96.12.31.1 Sierra Leone. (Fig. 20e)

Scotoecus hindei
BM(NH) 14.7.31.13 30 m NW of Baringo, Kenya. (Fig. 20d)
BM(NH) 66.1466 Jos, Nigeria (*falabae*). (Fig. 20b)

Scotoecus hirundo
BM(NH) 76.771 Mole National Park, Ghana. (Fig. 20c)

Scotoecus pallidus
BM(NH) 86.531 Afghanistan (damaged).

Philetor brachypterus
BM(NH) ——— New Guinea. (Fig. 16b)

Hesperoptenus (*Milithronycteris*)

Hesperoptenus blanfordi
BM(NH) 83.853 Sepilok, Sabah, Borneo, 5°52′N, 117°56′E. (Fig. 21g)

Hesperoptenus tickelli
BM(NH) 71.12.26.1 Sri Lanka. (Fig. 21b)

Hesperoptenus tomesi
BM(NH) 7.1.1.428 Malacca, Malaya (Holotype). (Fig. 21a)

Chalinolobus gouldi
BM(NH) 71.1504 Westwood, near Rockhampton, Queensland, Australia. (Fig. 17b)

Chalinolobus morio
BM(NH) 6.8.1.60 (King River, Western Australia. (Fig. 17a)

Chalinolobus nigrogriseus
BM(NH) 44.6.13.2 Port Essington, Northern Territory, Australia (*rogersi*).
BM(NH) 75.2260 Pine Creek, 20 m ESE of Gandy's Hill, Northern Territory, Australia, 13°49′S, 131°49′E. (*rogersi*). (Fig. 17c)

Chalinolobus picatus
BM(NH) 9.3.7.2 Gunnamulla, Queensland, Australia. (Fig. 17d)

Chalinolobus tuberculatus
BM(NH) 89.10.27.1 Outlying islands near Stewart I, New Zealand. (Fig. 17e)

Nyctophilinae

Nyctophilus bifax
BM(NH) 67.5.6.5 Cape York, Queensland, Australia.
BM(NH) 77.3.28.1 Islands of Torres Straits, Australia.
BM(NH) 86.11.8.12 Somerset, Cape York, Queensland, Australia.
BM(NH) 15.3.13.1 Cloncurry, Queensland, Australia.
BM(NH) 15.3.13.3 Herberton District, Queensland, Australia (Holotype). (Fig. 22a)

Nyctophilus daedalus
BM(NH) 47.7.21.16, BM(NH) ——— Port Essington, Northern Territory, Australia. (Fig. 22g, BM(NH) 47.7.21.16)
BM(NH) 97.4.12.5 Daly River, Northern Territory, Australia.

Nyctophilus gouldi
BM(NH) 15.3.13.7 Ash I, Hunter River, New South Wales, Australia (damaged, part lost).
BM(NH) 15.3.13.8 Sydney, New South Wales, Australia.
BM(NH) ——— Botany, Sydney, New South Wales, Australia (Original No. 164) (Fig. 22d)
HZM 1.12085 Werrikimbe, Hastingsshire, New South Wales, Australia. (Fig. 16c)
BM(NH) 52.1.15.30 Tasmania (*sherrini*). (Fig. 22f)

Nyctophilus geoffroyi
BM(NH) 15.3.13.11 Kosciusko, New South Wales, Australia (*pacificus*).
BM(NH) ——— Tasmania (*pacificus*) (Original No. M.1735).

BM(NH) ——— Launceston, Tasmania (*pacificus*) (Original No. M.168) (Fig. 22e)
BM(NH) 7.1.4.3 Alexandria, Northern Territory, Australia (*pallescens*). (Fig. 22b)

Nyctophilus microtis
BM(NH) 88.4.18.1 Sogeri, Papua New Guinea (Holotype). (Fig. 22c)

Pharotis imogene
BM(NH) 97.8.7.21 Kamali, Papua New Guinea. (Fig. 22h)

Table 1 Classification of the Vespertilioninae and Nyctophilinae.

Miller (1907)	Tate (1942*a*)	Simpson (1945)	Sokolov (1973)	Koopman (1984*a*, *b*, 1985)	Hill & Harrison
Vespertilioninae	Vespertilioninae	Vespertilioninae	Vespertilionidae	Vespertilioninae	Vespertilioninae
			(part)		
	Myotini			Myotini	Myotini
Myotis	*Myotis*	*Myotis*	*Myotis*	*Myotis*	*Myotis*
Pizonyx	*Pizonyx*	(Including	(Including	(Including	(Including
Lasionycteris	*Lasionycteris*	*Pizonyx*)	*Pizonyx*	*Pizonyx*	*Cistugo*
Pipistrellus	'Plecotini'	*Lasionycteris*	*Cistugo*)	*Cistugo*	*Anamygdon*)
Glischropus	*Plecotus*	*Pipistrellus*	*Lasionycteris*	*Anamygdon*)	*Pizonyx*
Scotozous	*Corynorhinus*	(Including	*Vespertilio*	*Lasionycteris*	*Lasionycteris*
Ia	*Idionycteris*	*Glischropus*	(Including	Vespertilionini	Plecotini
Pterygistes	*Euderma*	*Scotozous*	*Eptesicus*	*Eudiscopus*	*Plecotus*
[=*Nyctalus*]	Pipistrellini	*Nyctalus*	*Rhinopterus*	*Pipistrellus*	(Including
Eptesicus	*Eudiscopus*	*Ia*	*Hesperoptenus*	(Including	*Corynorhinus*)
Vespertilio	*Pipistrellus*	*Eptesicops*)	*Tylonycteris*	*Ia*	*Idionycteris*
Rhinopterus	*Glischropus*	*Eudiscopus*	*Mimetillus*	*Scotozous*)	*Euderma*
Hesperoptenus	*Nyctalus*	*Eptesicus*	*Philetor*	*Nyctalus*	*Barbastella*
Tylonycteris	*Ia*	(Including or	*Histiotus*	*Glischropus*	*Rhogeessa*
Mimetillus	*Scotozous*	closely allied	*Laephotis*	*Eptesicus*	*Baeodon*
Philetor	*Chalinolobus*	to	*Pipistrellus*	(Including	*Nycticeius*
Histiotus	*Glauconycteris*	*Rhinopterus*	*Scotozous*	*Rhinopterus*)	*Otonycteris*
Laephotis	*Barbastella*	*Hesperoptenus*	*Ia*	*Vespertilio*	Lasiurini
Otonycteris	*Philetor*	*Tylonycteris*	*Glischropus*)	*Laephotis*	*Lasiurus*
Nycticeius	*Mimetillus*	*Mimetillus*	*Nyctalus*	*Histiotus*	*Dasypterus*
Scotoecus	*Tylonycteris*	*Philetor*	*Eudiscopus*	*Philetor*	Antrozoini
Scoteinus	*Hesperoptenus*	*Histiotus*	*Otonycteris*	*Tylonycteris*	*Antrozous*
[=*Scotomanes*]	*Vespertilio*	*Laeophotis*)	*Nycticeius*	*Mimetillus*	*Bauerus*
[*Scoteanax*]	*Eptesicus*	*Vespertilio*	(Including	*Hesperoptenus*	Scotophilini
[*Scotorepens*]	*Rhinopterus*	*Otonycteris*	*Scotoecus*	*Chalinolobus*	*Scotomanes*
Scotomanes	*Laephotis*	*Nycticeius*	*Scotomanes*	(Including	[*Scoteinus*]
Rhogeessa	*Histiotus*	(Including	*Scoteinus*	*Glauconycteris*)	*Scotophilus*
Pachyotus	Nycticeini	*Scotoecus*	[=*Scotomanes*]	Nycticeini	Vespertilionini
[=*Scotophilus*]	*Scoteinus*	*Scoteinus*	[*Scoteanax*]	*Nycticeius*	*Eptesicus*

Table 1–*cont.*

Miller (1907)	Tate (1942*a*)	Simpson (1945)	Sokolov (1973)	Koopman (1984*a*, *b*, 1985)	Hill & Harrison
Chalinolobus	[=*Scotomanes*]	[=*Scotomanes*]	[*Scotorepens*]	[*Scoteanax*]	(Including
Glauconycteris	[*Scoteanax*]	[*Scoteanax*]	*Rhogeessa*	[*Scotorepens*]	*Rhinopterus*)
Lasiurus	[*Scotorepens*]	[*Scotorepens*]	(Including	*Rhogeessa*	*Vespertilio*
Dasypterus	*Nycticeius*	*Scotomanes*)	*Baeodon*)	(Including	*Histiotus*
Barbastella	*Rhogeessa*	*Rhogeessa*	*Scotophilus*	*Baeodon*)	*Ia*
Plecotus	*Baeodon*	(Including	*Chalinolobus*	*Scotoecus*	*Tylonycteris*
Corynorhinus	*Scotoecus*	*Baeodon*)	(Including	*Scotomanes*	*Mimetillus*
Euderma	*Scotophilus*	*Scotophilus*	*Glauconycteris*)	[*Scoteinus*]	*Glauconycteris*
Nyctophilinae	*Scotomanes*	*Chalinolobus*	*Lasiurus*	*Scotophilus*	Pipistrellini
Antrozous	*Otonycteris*	(Including	(Including	*Otonycteris*	(?) *Eudiscopus*
Nyctophilus	Lasiurini	*Glauconycteris*)	*Dasypterus*)	Lasiurini	*Pipistrellus*
	Lasiurus	*Cistugo*	*Barbastella*	*Lasiurus*	*Laephotis*
	Dasypterus	*Lasiurus*	*Plecotus*	(Including	*Glischropus*
		(Including	(Including	*Dasypterus*)	*Scotozous*
	Nyctophilinae	*Dasypterus*)	*Corynorhinus*	Plecotini	*Scoteanax*
	Nyctophilus	*Barbastella*	*Idionycteris*)	*Barbastella*	*Scotorepens*
	Pharotis	*Plecotus*	*Euderma*	*Plecotus*	*Nycticeinops*
	Antrozous	(Including	*Antrozous*	(Including	
		Corynorhinus)	*Nyctophilus*	*Corynorhinus*	*Scotoecus*
		Idionycteris	(Including	*Idionycteris*)	*Nyctalus*
		Euderma	*Pharotis*)	*Euderma*	*Philetor*
					Hesperoptenus
		Nyctophilinae		Antrozoini	*Chalinolobus*
		Antrozous		*Bauerus*	
		Nyctophilus		*Antrozous*	
					Nyctophilinae
				Nyctophilini	
				Nyctophilus	*Nyctophilus*
				(Including	(Including
				Lamingtona)	*Lamingtona*)
				Pharotis	*Pharotis*

Table 2 Usual incisive and premolar dental formulae in the Vespertilioninae and Nyctophilinae. Total number of teeth (including four canines and twelve molars) in parentheses. Dental notation of Miller (1907).

i $\frac{-}{1}\frac{2}{2}\frac{3}{3}$, pm $\frac{-}{-}\frac{2}{2}\frac{3}{3}\frac{4}{4}$	(38)	*Myotis, Pizonyx*
i $\frac{-}{1}\frac{2}{2}\frac{3}{3}$, pm $\frac{-}{-}\frac{2}{2}\frac{-}{3}\frac{4}{4}$	(36)	*Lasionycteris, Plecotus, Idionycteris, Eudiscopus*
i $\frac{-}{1}\frac{2}{2}\frac{3}{3}$, pm $\frac{-}{-}\frac{2}{2}\frac{-}{-}\frac{4}{4}$	(34)	*Euderma, Barbastella, Ia, Pipistrellus, Glischropus, Scotozous, Nyctalus, Chalinolobus*
i $\frac{-}{1}\frac{2}{2}\frac{3}{3}$, pm $\frac{-}{-}\frac{-}{2}\frac{-}{-}\frac{4}{4}$	(32)	*Eptesicus, Vespertilio, Histiotus, Tylonycteris, Mimetillus, Glauconycteris, Pipistrellus, Laephotis, Philetor, Hesperoptenus*
i $\frac{-}{1}\frac{2}{2}\frac{-}{3}$, pm $\frac{-}{-}\frac{2}{2}\frac{-}{-}\frac{4}{4}$	(32)	*Lasiurus*
i $\frac{-}{1}\frac{2}{2}\frac{-}{3}$, pm $\frac{-}{-}\frac{-}{2}\frac{-}{-}\frac{4}{4}$	(30)	*Rhogeessa, Baeodon, Nycticeius, Otonycteris, Dasypterus, Scotomanes, Scotophilus, Scoteanax, Scotorepens, Nycticeinops, Scotoecus, Nyctophilus, Pharotis*
i $\frac{-}{1}\frac{2}{2}\frac{-}{-}$, pm $\frac{-}{-}\frac{-}{2}\frac{-}{-}\frac{4}{4}$	(28)	*Antrozous, Bauerus*

Table 3 Classifications of the Vespertilioninae and Nyctophilinae. That of Tate (1942*a*) is concerned primarily with Oriental and Australasian taxa, those of Koopman with Australasian (1973) and predominantly African (1975) forms.

Tate (1942*a*)	Koopman (1973, 1975)	Hill & Harrison
Pipistrellus	*Pipistrellus*	*Pipistrellus*
abramus group	Amalgamates *pipistrellus, abramus* (=*javanicus*), *coromandra* and *tenuis* groups of Tate (1942*a*)	*Pipistrellus* (*Pipistrellus*)
abramus	*pipistrellus* group	*pipistrellus* group
akokomuli	*imbricatus*	*pipistrellus* subgroup
bancanus	*javanicus* (Including *abramus*)	*pipistrellus* (Including *aladdin, bactrianus, lacteus, mediterraneus*)
camortae	*meyeni*	*nathusii*
irretitus	*nanus* (Including (?) *helios*)	*permixtus*
paterculus	*permixtus*	*javanicus* subgroup
pumiloides	*tenuis* (Including *angulatus, collinus, nitidus, papuanus, ponceleti, murrayi, sewelanus, subulidens, westralis* [Koopman, 1984*c*])	*abramus* (Including *akokomuli, irretitus, pumiloides*)
pipistrellus group		*babu*
pipistrellus (Including *bactrianus*)		*endoi*
nathusii		*javanicus* (Including *bancanus, camortae, meyeni, 'tralatitius'*)
coromandra group		*paterculus*
aladdin		*peguensis*
angulatus		*coromandra* subgroup
collinus		*adamsi*
coromandra		*angulatus* (Including *ponceleti*)
imbricatus		*collinus*
meyeni		*coromandra* (Including *afghanus, portensis, tramatus*)
micropus		*mimus* (Including *glaucillus, principulus*)
murrayi		*murrayi*
ponceleti		*papuanus*
portensis		*sturdeei*
regulus		*tenuis* (Including *nitidus, sewelanus, subulidens*)
sturdeei		*wattsi*
subulidens		*westralis*
tramatus		*ceylonicus* subgroup
tenuis group		*ceylonicus* (Including *borneanus, chrysothrix, indicus, raptor, shanorum, subcanus*)
mimus (Including *glaucillus*)		(?) *minahassae*
nitidus		
papuanus (Including *orientalis*)		
principulus		
tenuis		
ceylonicus group	*ceylonicus* group	
ceylonicus (Including *chrysothrix, indicus, subcanus*)	*ceylonicus*	

Table 3–*cont.*

Tate (1942*a*)	Koopman (1973, 1975)	Hill & Harrison
minahassae group	*minahassae* group	
minahassae	*minahassae*	
rueppellii group	*rueppellii* group	*rueppellii* group
coxi	*rueppellii* (Including (?)	*crassulus*
	fuscipes; *pulcher*)	*nanulus*
		rueppellii (Including *coxi,*
		fuscipes, leucomelas, pulcher,
		senegalensis, vernayi)
kuhlii group	*kuhlii* group	*kuhlii* group
babu	*aero*	*aero*
canus	*anchietae*	*deserti*
kuhlii (Including	*deserti*	*inexspectatus*
ikhwanius, lepidus)	*inexspectatus*	*kuhlii* (Including (?)
leucotis	*kuhlii* (Including (?)	*aegyptius*; *fuscatus,*
lobatus	*aegyptius*; *fuscatus*)	*ikhwanius*)
	rusticus (Including *marrensis*)	*maderensis*
		rusticus (Including *marrensis*)
Eptesicus		*Pipistrellus* (*Vespadelus*)
pumilus group		*douglasorum*
pumilus (Including		*pumilus* (Including
caurinus, darlingtoni,		*darlingtoni*)
vulturnus)		*regulus*
pygmaeus		*sagittula*
		vulturnus
		Pipistrellus (*Perimyotis*)
		subflavus
Pipistrellus		*Pipistrellus* (*Hypsugo*)
savii group	*savii* group	*savii* group
austenianus	*ariel*	*savii* subgroup
cadornae	*macrotis*	*anchietae* (= *'bicolor'* ?)
curtatus	*maderensis*	*ariel*
macrotis		*austenianus*
savii		*bodenheimeri*
vordermanni		*savii* (Including *caucasicus,*
		darwini, maurus)
		nanus subgroup
		arabicus
		helios
		musciculus
		nanus (Including *culex,*
		stampflii)
		pulveratus subgroup
		pulveratus
	hesperus group	*hesperus* subgroup
	hesperus	*hesperus*
	musciculus	*eisentrauti* subgroup
		eisentrauti
		imbricatus subgroup
		curtatus
		imbricatus
		macrotis
		vordermanni
		lophurus subgroup
		cadornae
		kitcheneri
		lophurus
joffrei group	*joffrei* group	*stenopterus* group
anthonyi	*stenopterus*	*anthonyi*
joffrei		*joffrei*
stenopterus		*stenopterus*

Table 3–*cont.*

Tate (1942*a*)	Koopman (1973, 1975)	Hill & Harrison
affinis group	*affinis* group	*Pipistrellus* (*Falsistrellus*)
affinis	*kitcheneri*	*affinis* group
kitcheneri	*petersi*	*affinis*
lophurus		(?) *mordax*
petersi		*petersi*
pulveratus		
tasmaniensis group		*tasmaniensis* group
tasmaniensis (Including		*mackenziei*
krefftii)		*tasmaniensis* (Including
		krefftii)
	Eptesicus	*Pipistrellus* (*Neoromicia*)
	capensis group	*capensis* group
	brunneus	*brunneus*
	capensis (= *notius*) (Including	*capensis* (Including *garambae*
	garambae, *grandidieri*)	*grandidieri*, *notius*, *matroka*)
	guineensis (Including	*guineensis* (Including
	(?) *rectitragus*)	*rectitragus*)
	melckorum	*melckorum*
	somalicus (Including *ugandae*,	*somalicus* (Including
	vansoni, *zuluensis*)	*ugandae*)
		zuluensis (Including *vansoni*)
	tenuipinnis group	*tenuipinnis* group
	flavescens (= *angolensis*)	*flavescens* (Including *angolensis*)
	rendalli (Including	*rendalli* (Including
	faradjius, *phasma*)	*faradjius*, *phasma*)
	tenuipinnis (Including *ater*)	*tenuipinnis* (Including *ater*)
	Pipistrellus	*Pipistrellus* (*Arielulus*)
circumdatus group	*circumdatus* group	*circumdatus*
circumdatus	*circumdatus*	*cuprosus*
mordax	*mordax*	*societatis*
Eptesicus	*Eptesicus*	*Eptesicus*
Eptesicus (*Amblyotus*)		*Eptesicus* (*Eptesicus*)
alaschanicus		*nilssonii* group
bobrinskoi		*bobrinskoi*
		gobiensis (Including
		centrasiaticus, *kashgaricus*)
matschiei (Including		*nilssonii* (Including *japonensis*,
pellucens)		(?) *parvus*; *propinquus*)
nilssonii (Including		*nasutus* group
caucasicus, *centrasiaticus*,		*nasutus* (Including *batinensis*
gobiensis, *kashgaricus*,		*matschiei*, *pellucens*,
pallescens, *tamerlani*, *velox*)		*walli*)
tauricus		
walli [*alaschanicus*,		
caucasicus, *pallescens*,	*serotinus* group	*serotinus* group
tamerlani, *tauricus*,	*bottae* (Including *innesi*)	*serotinus* subgroup
velox allocated to	*hottentotus* (= *megalurus*)	*bottae* (Including *anatolicus*,
Pipistrellus savii by	(Including *smithi*)	*hingstoni*, *innesi*, *ognevi*,
Kuzyakin, 1950]	*loveni*	*omanensis*)
Eptesicus (*Rhyneptesicus*)	*platyops*	*brasiliensis* (Incluidng *andinus*,
nasutus group	*serotinus* (Including	*argentinus*, *chiriquinus*,
nasutus	*isabellinus*)	*melanopterus*)
Eptesicus (*Eptesicus*)		*diminutus* (Including
fuscus group		*dorianus*, *fidelis*)
bottae		*furinalis* (Including *inca*,
hingstoni		*montosus*)
serotinus (Including		*fuscus* (Including *hispaniolae*,
andersoni, *brachydigitus*,		*peninsulae*)
mirza, *pachyomus*, *pallens*,		*guadeloupensis*
shirazensis, *sinensis*)		*hottentotus* (= *megalurus*)

Table 3–*cont.*

Tate (1942*a*)	Koopman (1973, 1975)	Hill & Harrison
sodalis (Including *ognevi*)		(Including *smithi*)
		innoxius (Including *punicus*)
		loveni
		lynni
		serotinus (Including *andersoni, brachydigitus, horikawai, intermedius, isabellinus, mirza, pachyomus, pallens, pashtomus, platyops, shirazensis, sinensis, sodalis, turcomanus*)
demissus group		*tatei*
demissus		*demissus* subgroup
Eptesicus (*Pareptesicus*)		*demissus*
pachyotis group		(?) *pachyotis* subgroup
pachyotis		*pachyotis*
	floweri group	*Eptesicus* (*Rhinopterus*)
	floweri (= *lowei*)	*floweri* (Including *lowei*)

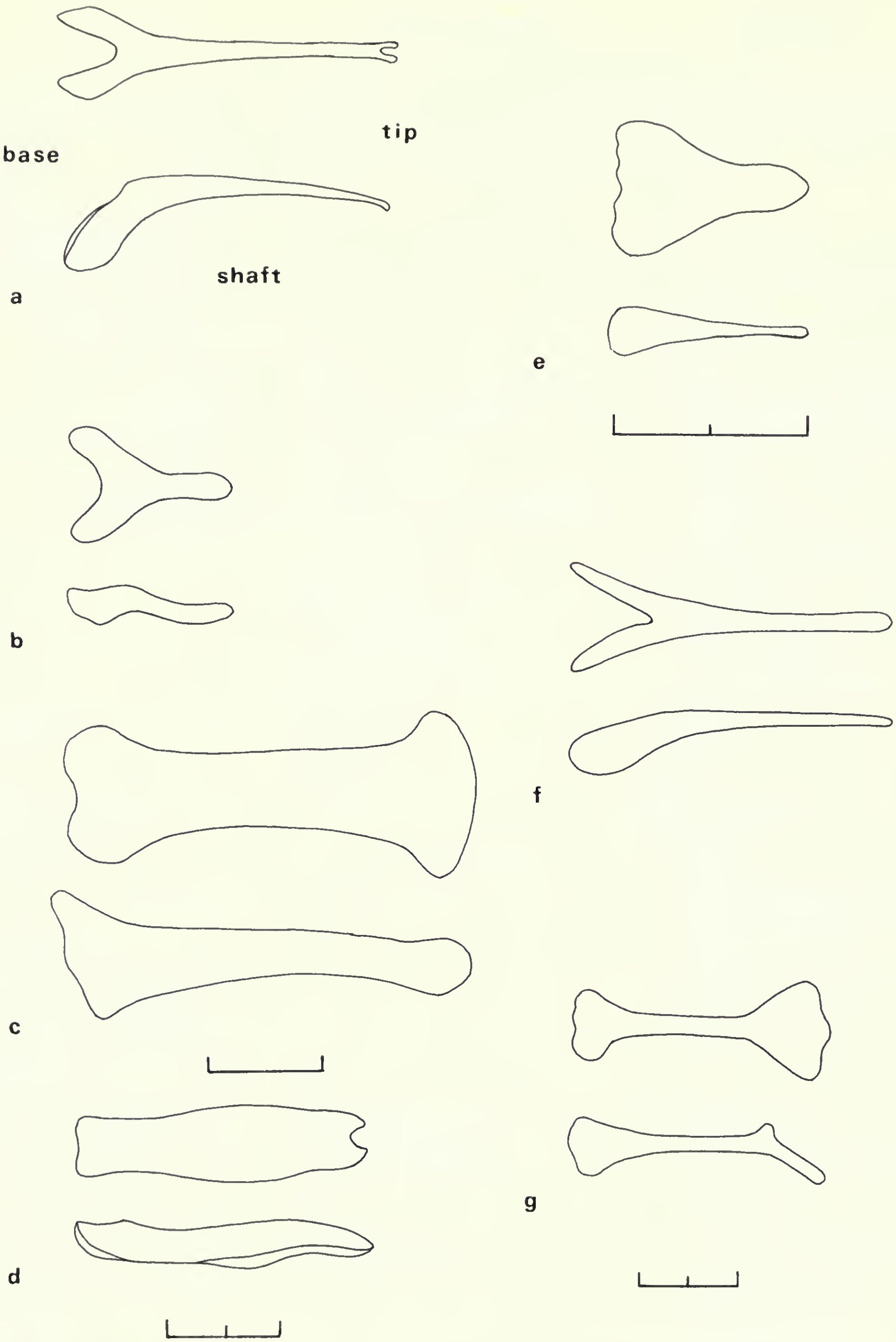
base
tip
shaft
a
b
c
d
e
f
g

Fig. 1 Bacular types in *Pipistrellus* and *Eptesicus* (see text). Scale a–c = 0·5 mm; d–g = 1 mm.

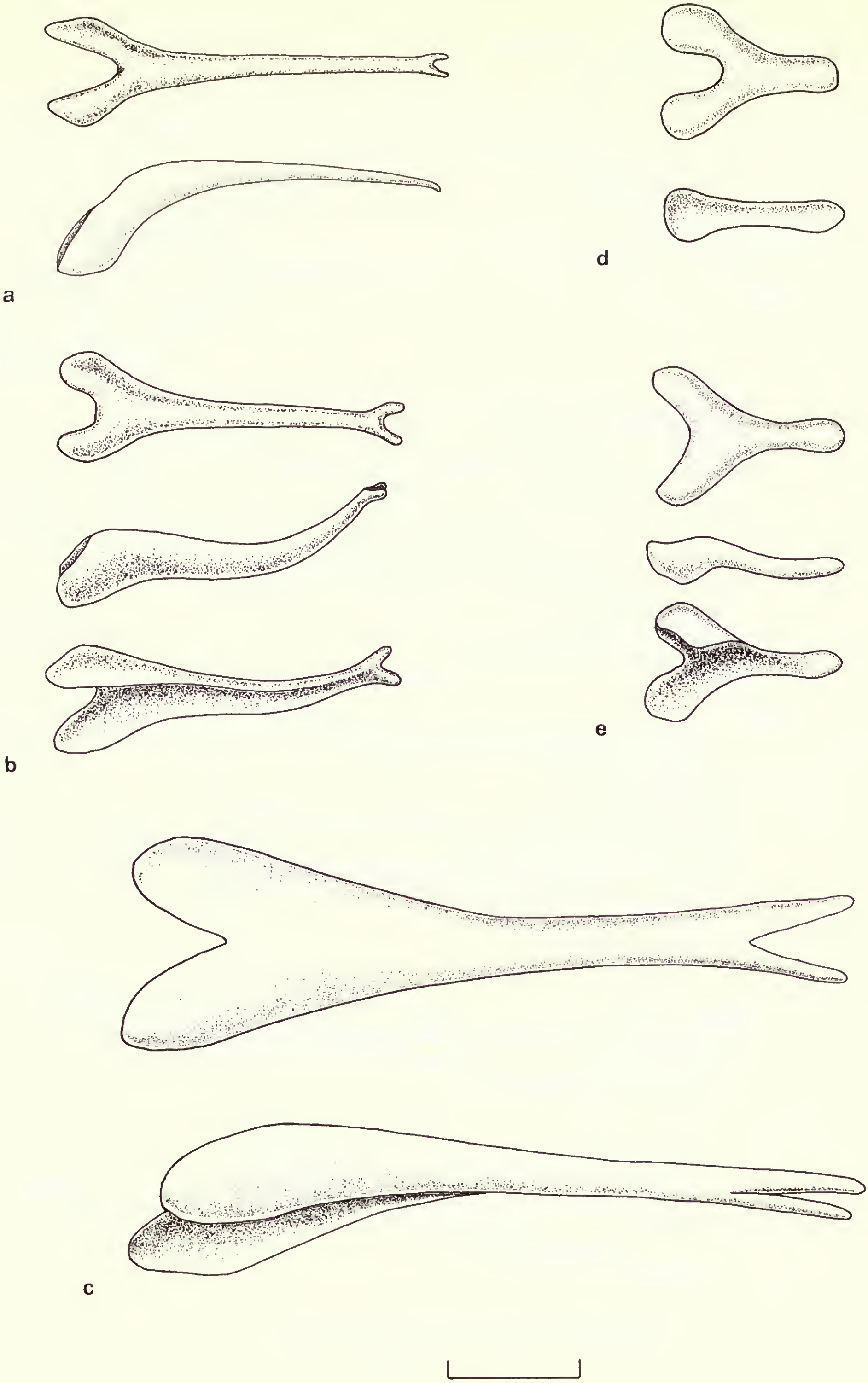

Fig. 2 Baculum of a, *Pipistrellus pipistrellus* (D, LL, reversed); b, *P. nathusii* (D, RL, RVL); c, *P. papuanus* (D, RL); d, *P. subflavus* (D, RL); e, *P. circumdatus* (D, LL, RVL). Scale = 0·5 mm.

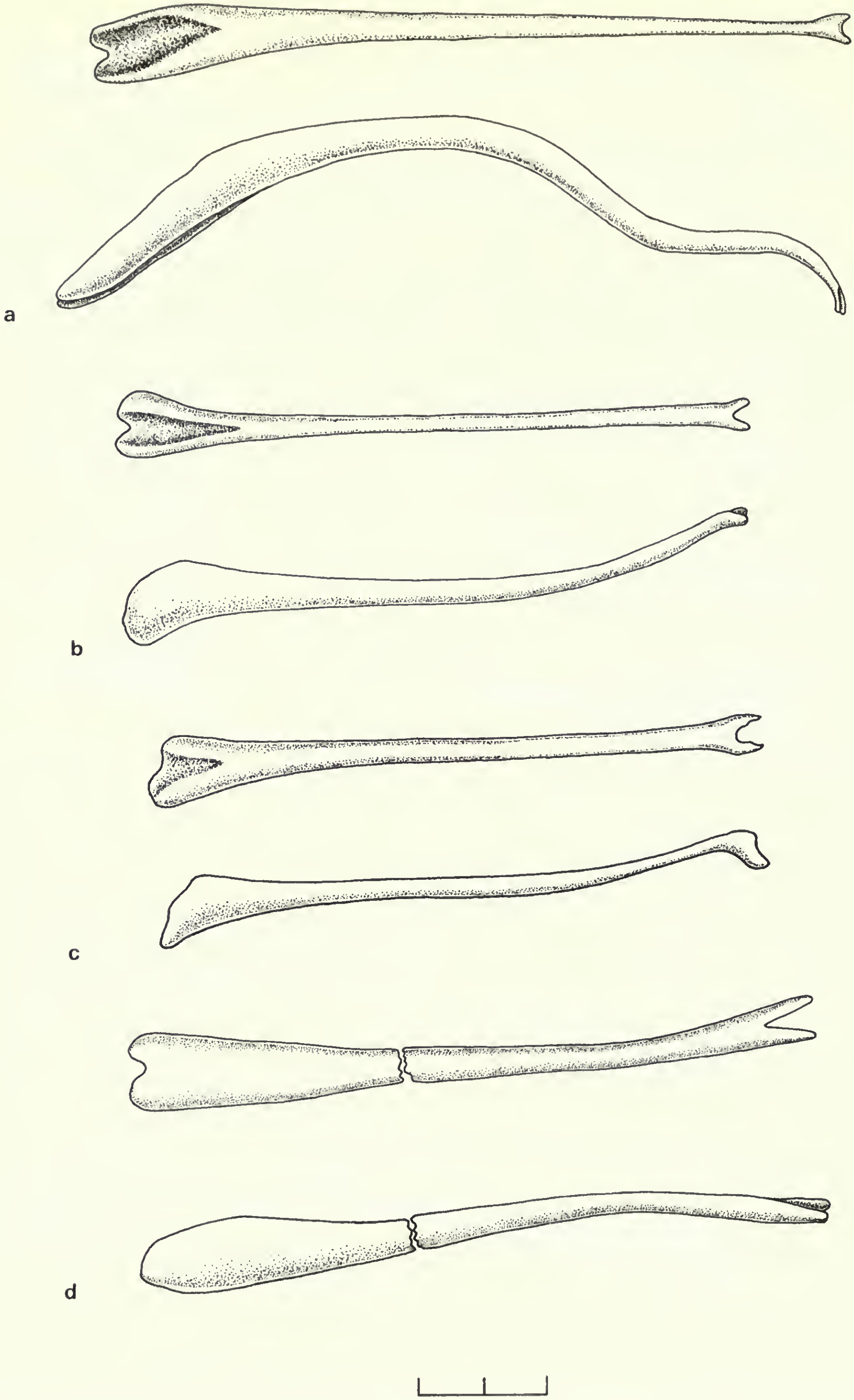

Fig. 3 Baculum (D, RL) of a, *Pipistrellus abramus*; b, *P. endoi*; c, *P. paterculus*; d, *P. ceylonicus* (*raptor*). Scale = 2 mm.

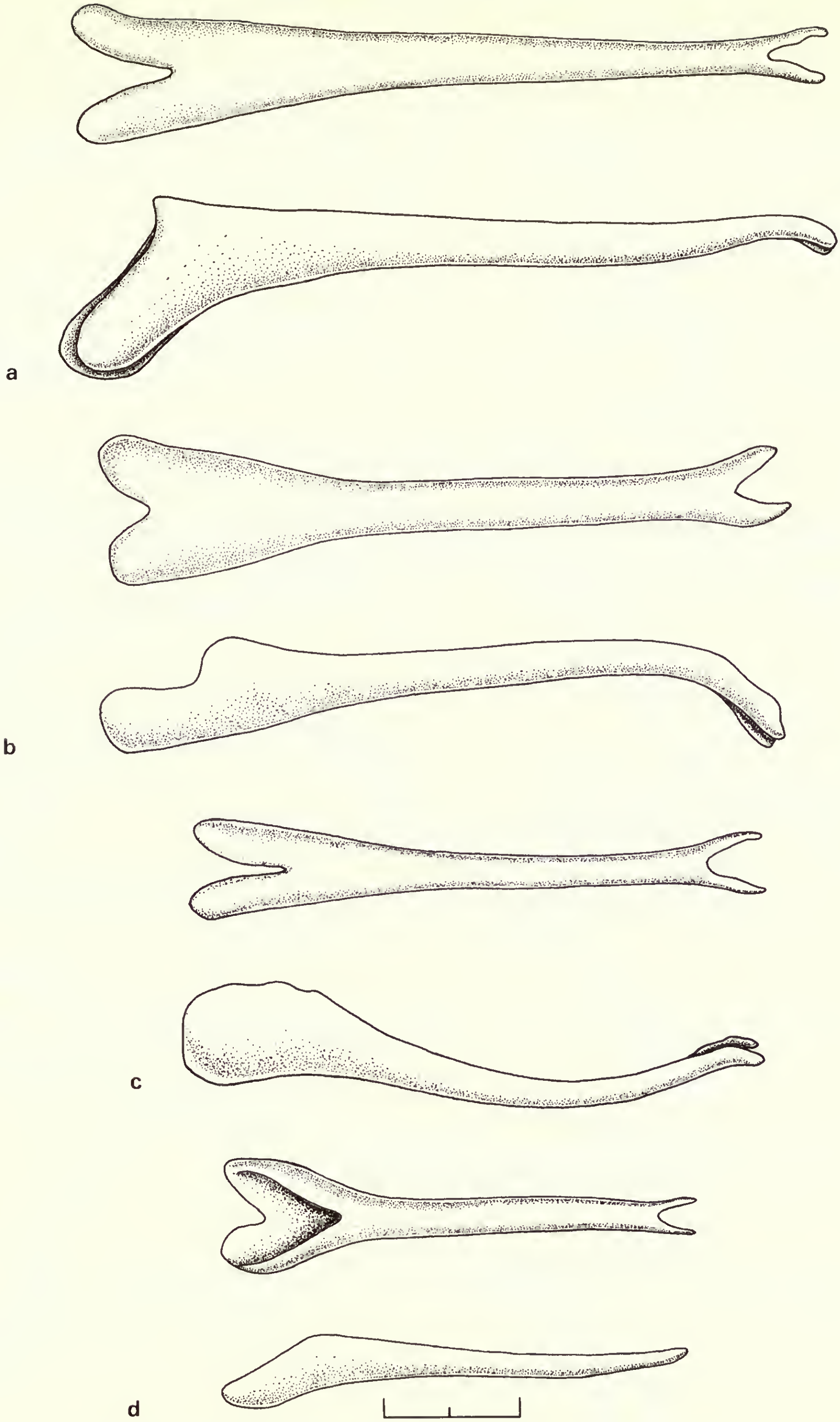

Fig. 4 Baculum (D, RL) of a, *Pipistrellus babu*; b, *P. collinus*; c, *P. murrayi*; d, *P. angulatus* (*ponceleti*). Scale = 1 mm.

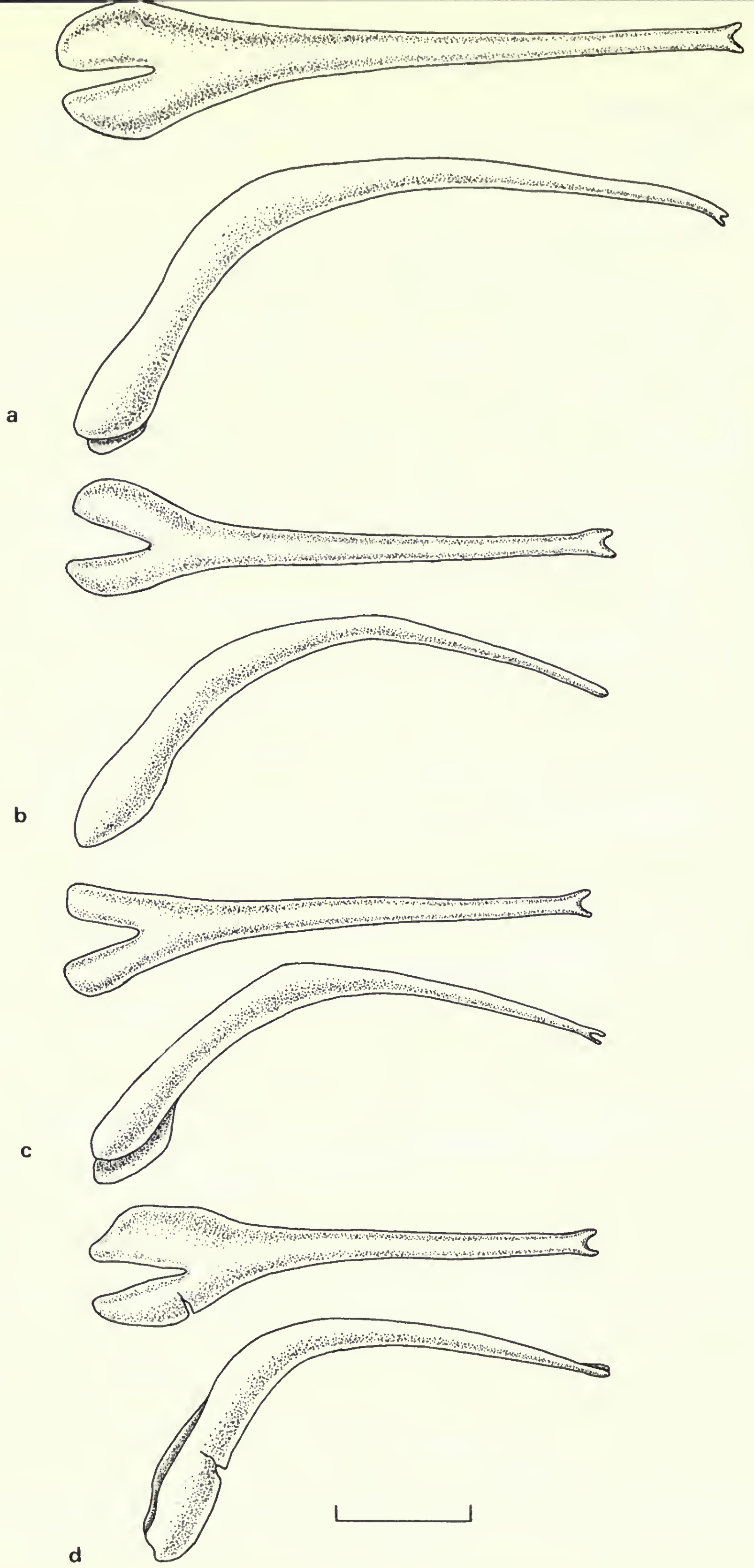

Fig. 5 Baculum (D, RL) of a, *Pipistrellus kuhlii*; b, *P. maderensis*; c, *P. deserti*; d, *P. rusticus*. Scale = 0·5 mm.

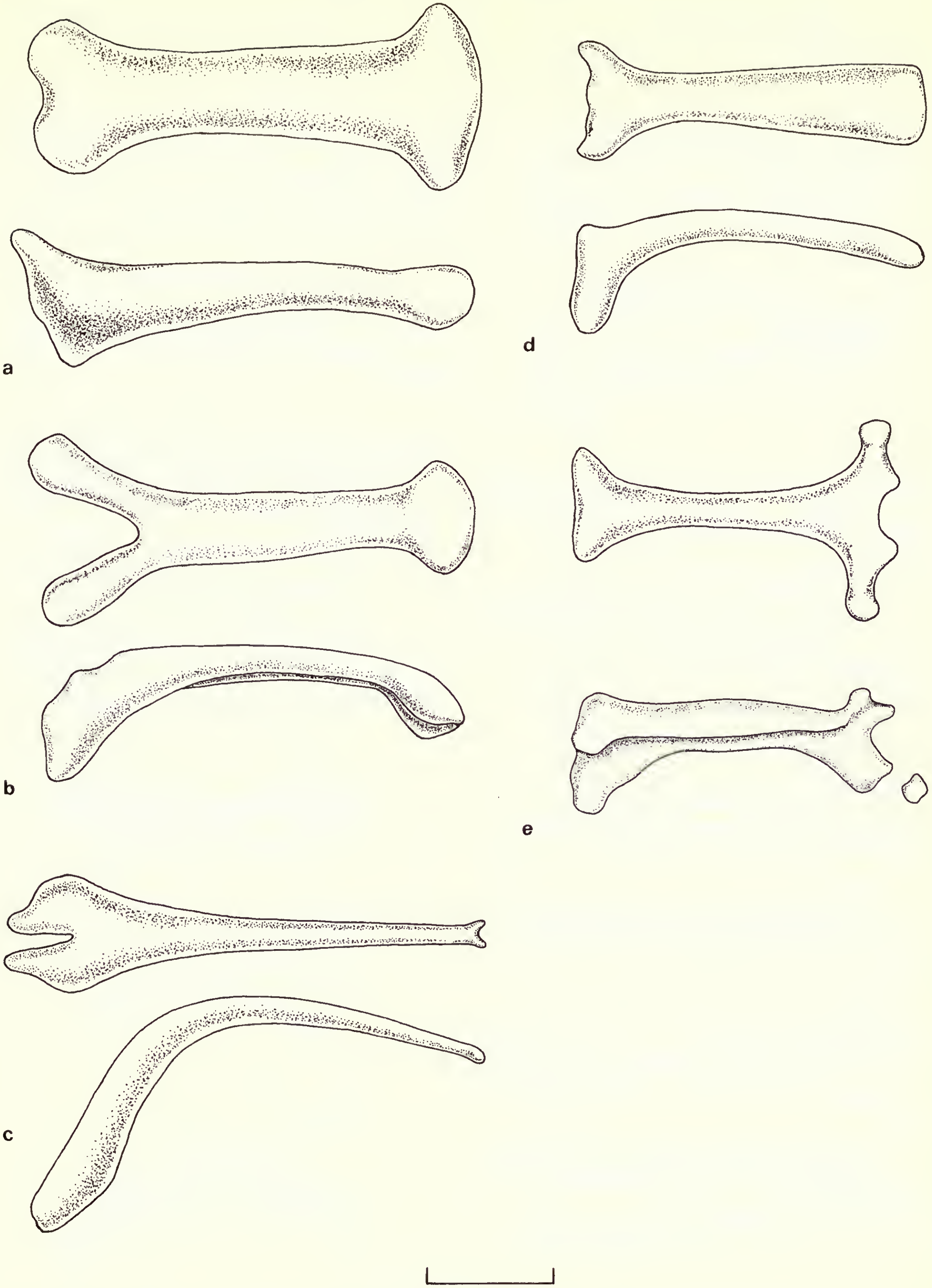

Fig. 6 Baculum of a, *Pipistrellus savii* (D, RL); b, *P. nanus* (D, RL); c, *P. rusticus* (D, RL); d, *P. helios* (D, RL); e, *P. anchietae* (D, LVL, reversed). Scale = 0·5 mm.

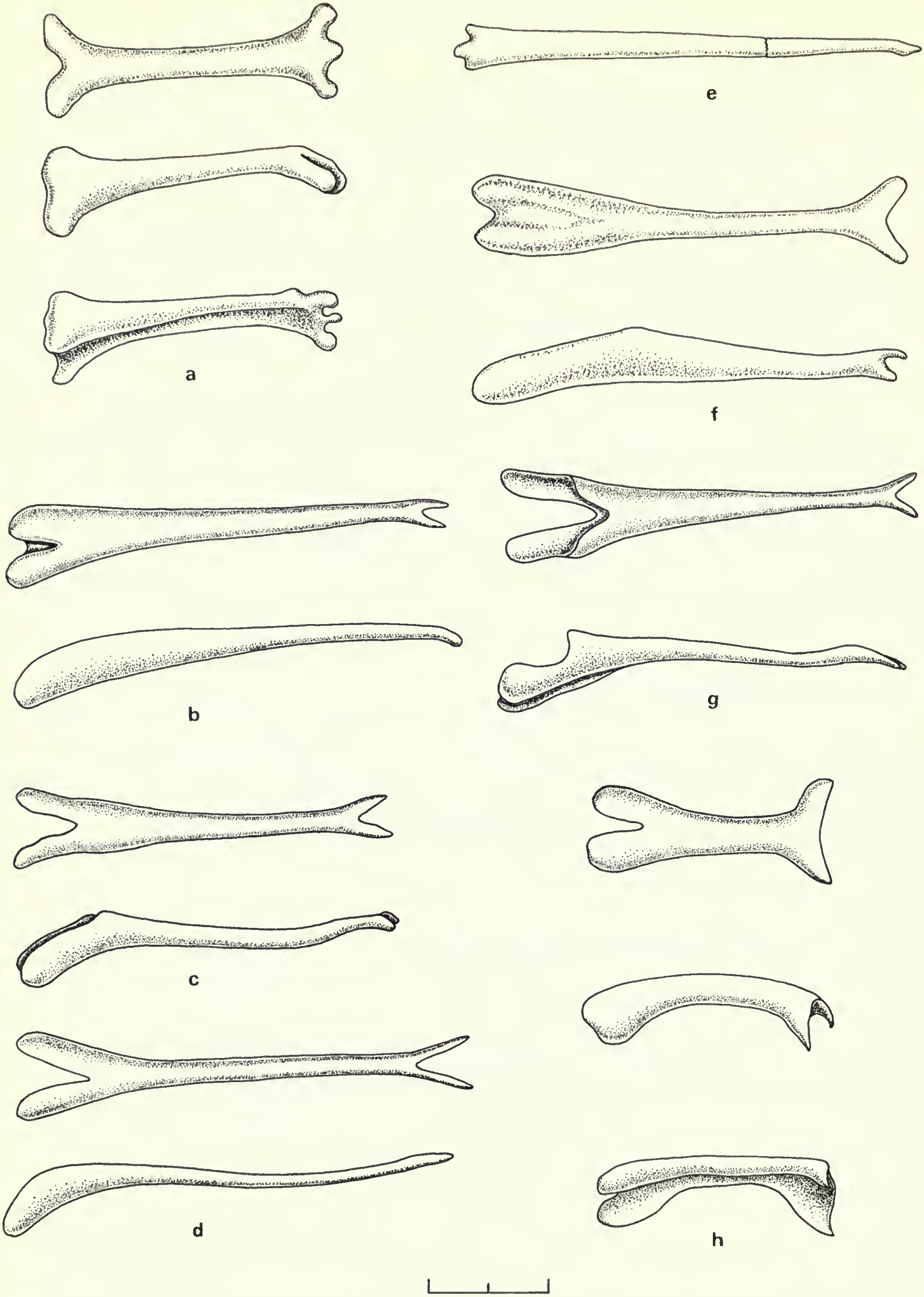

Fig. 7 Baculum of a, *Pipistrellus arabicus* (D, RL, RVL); b, *P. coromandra* (*tramatus*) (D, RL); c, *P. coromandra* (D, RL); d, *P. ceylonicus* (D, RL); e, *P. crassulus* (D); f, *P. nanulus* (D, RL); g, *P. mimus* (D, RL); h, *P. stenopterus* (D, RL, RVL). Scale = 1 mm.

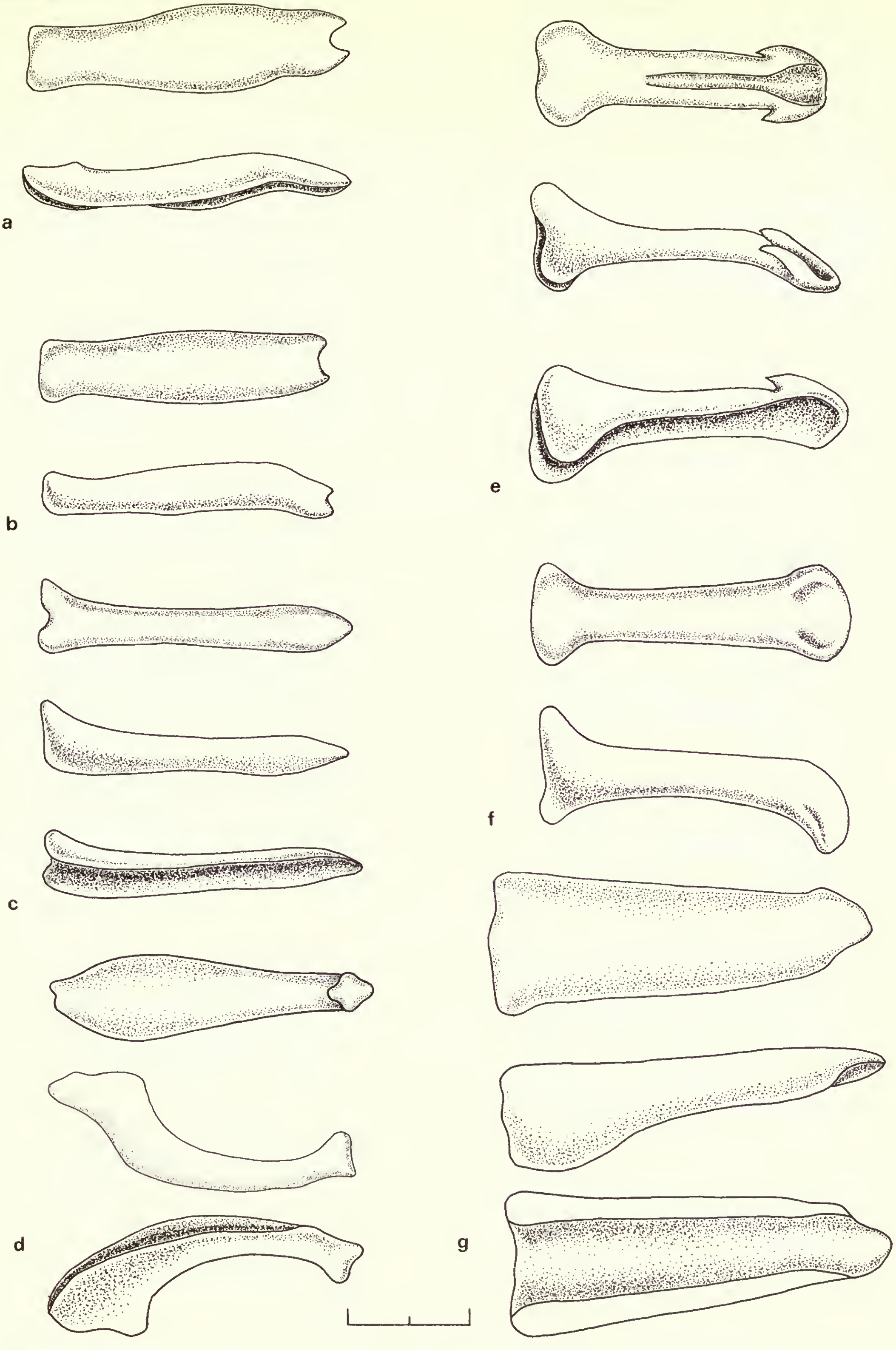

Fig. 8 Baculum of a, *Pipistrellus affinis* (D, RL); b, *P. petersi* (D, RL); c, *P. pulveratus* (D, RL, RVL); d, *P. hesperus* (D, LL, reversed, LVL); e, *P. kitcheneri* (D, RL, RVL); f, *P. lophurus* (D, RL); g, *P. tasmaniensis* (D, RL, V). Scale = 1 mm.

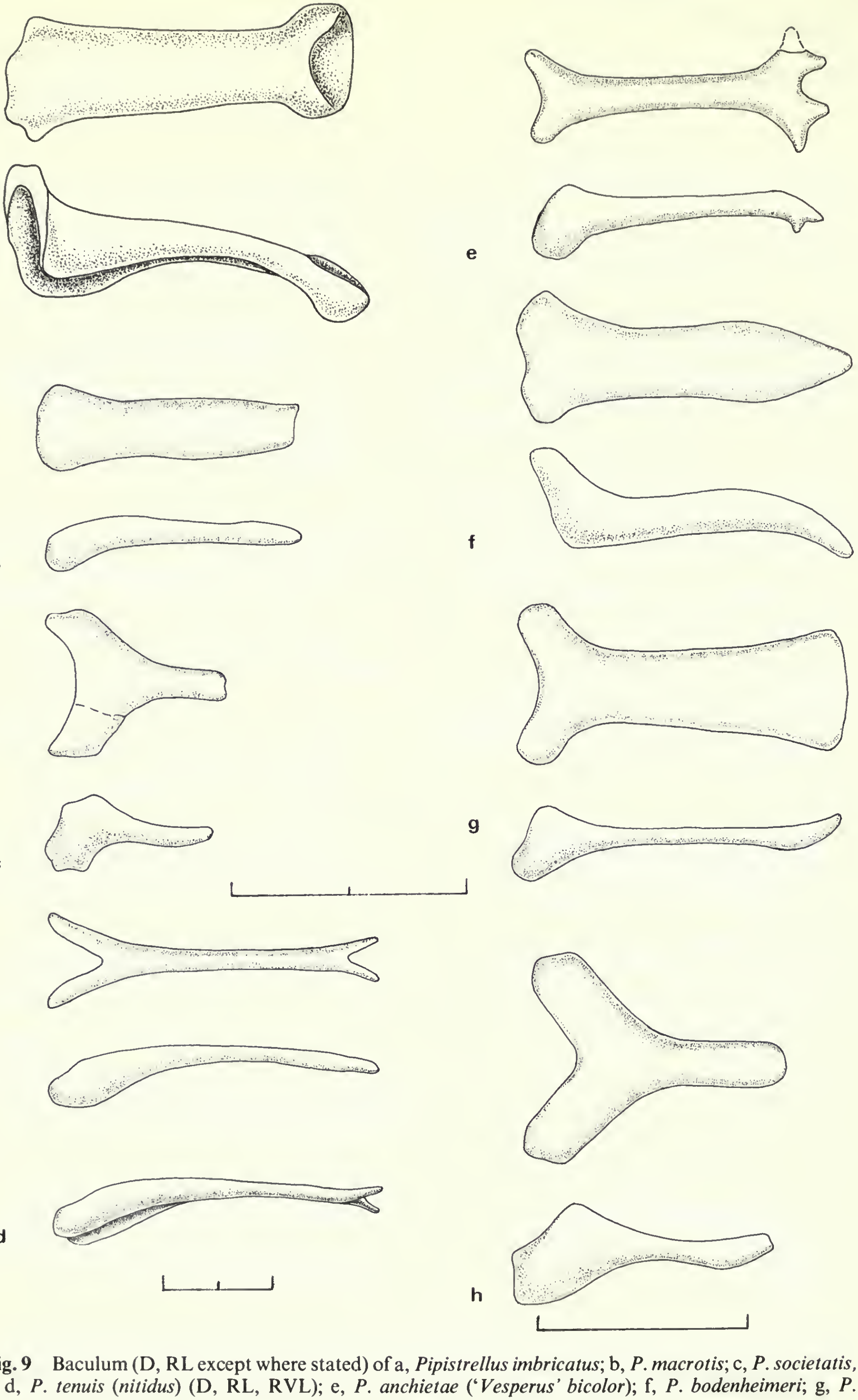

Fig. 9 Baculum (D, RL except where stated) of a, *Pipistrellus imbricatus*; b, *P. macrotis*; c, *P. societatis*, d, *P. tenuis* (*nitidus*) (D, RL, RVL); e, *P. anchietae* ('*Vesperus*' *bicolor*); f, *P. bodenheimeri*; g, *P. eisentrauti*; h, *P. cuprosus*. Scales a–g = 1 mm; h = 0·5 mm.

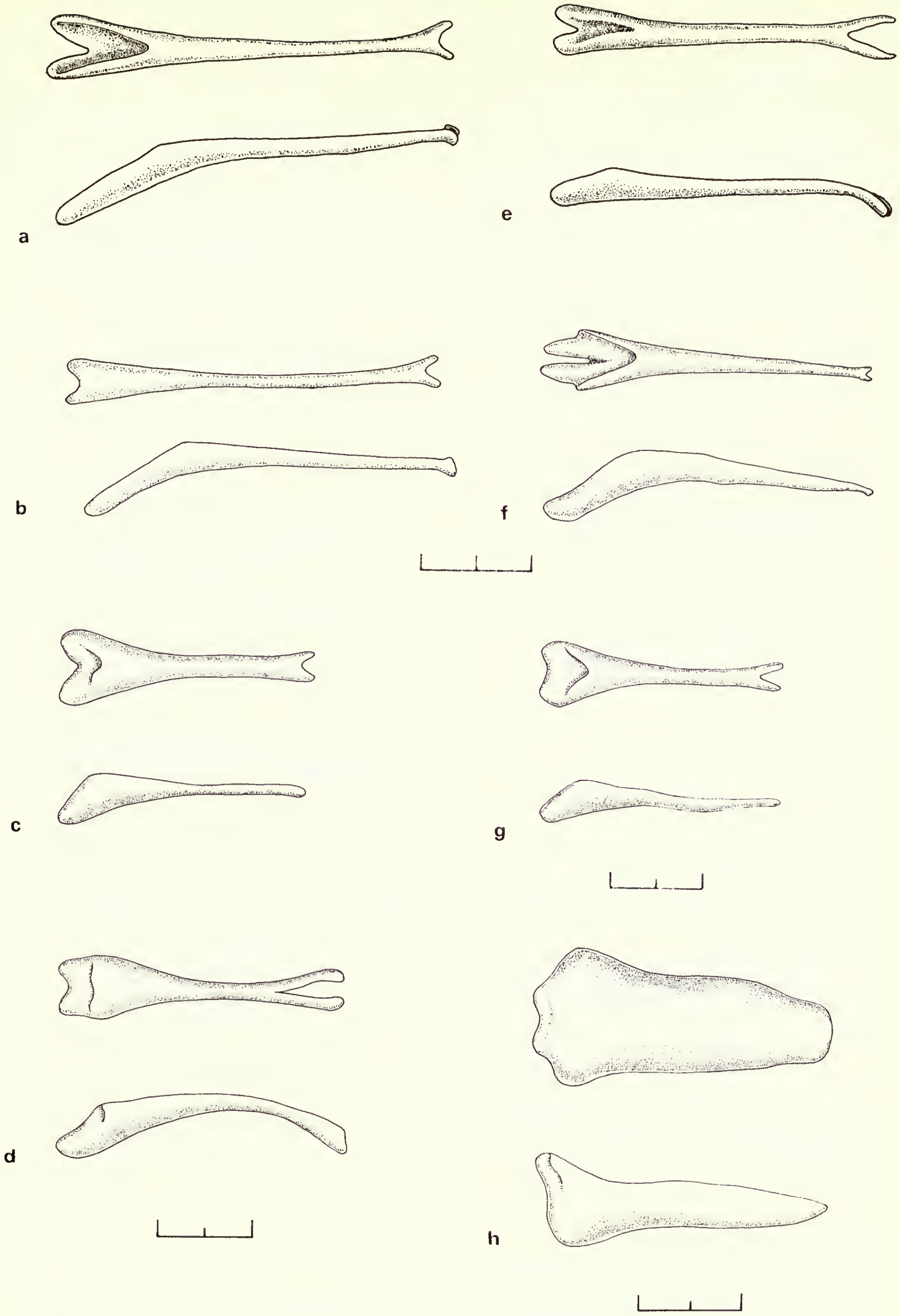

Fig. 10 Baculum (D, RL) of a, *Pipistrellus rueppellii* (*pulcher*); b, *P. rueppellii*; c, *P. adamsi*; d, *P. westralis*; e, *P. javanicus*; f, *Nyctalus noctula*; g, *P. wattsi*; h, *P. mackenziei* (c, d, g, h from Kitchener *et al.*, 1986). Scales = a, b, e, f = 2 mm; c, d, g, h = 1 mm.

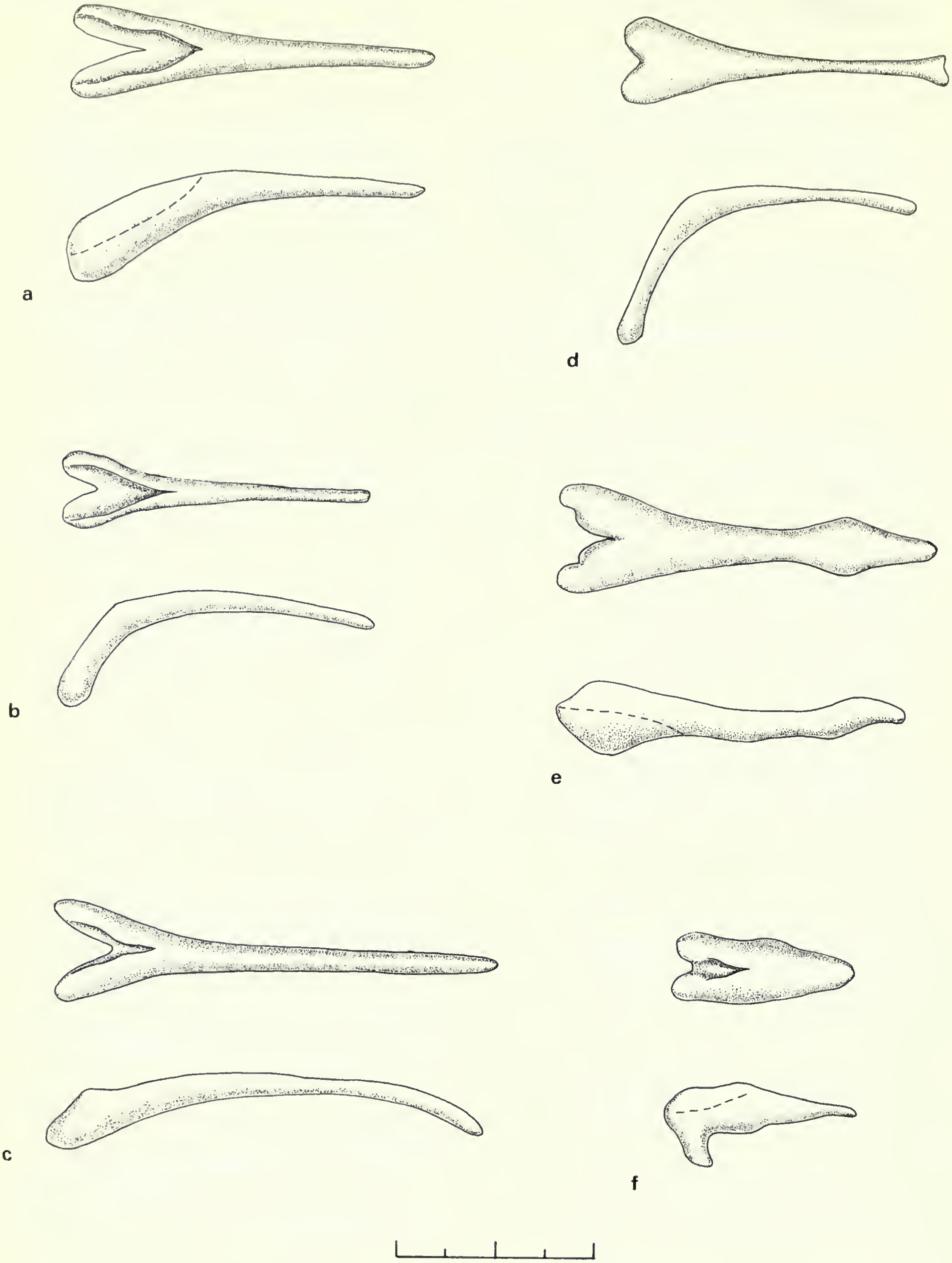

Fig. 11 Baculum (V, RL) of a, *Pipistrellus pumilus pumilus*; b, *P. pumilus* (*caurinus*); c, *P. vulturnus*; d, *P. douglasorum*; e, *P. regulus*; f, *P. sagittula* (a–c, e, f from McKean *et al.*, 1970; d from Kitchener, 1976). Scale = 2 mm.

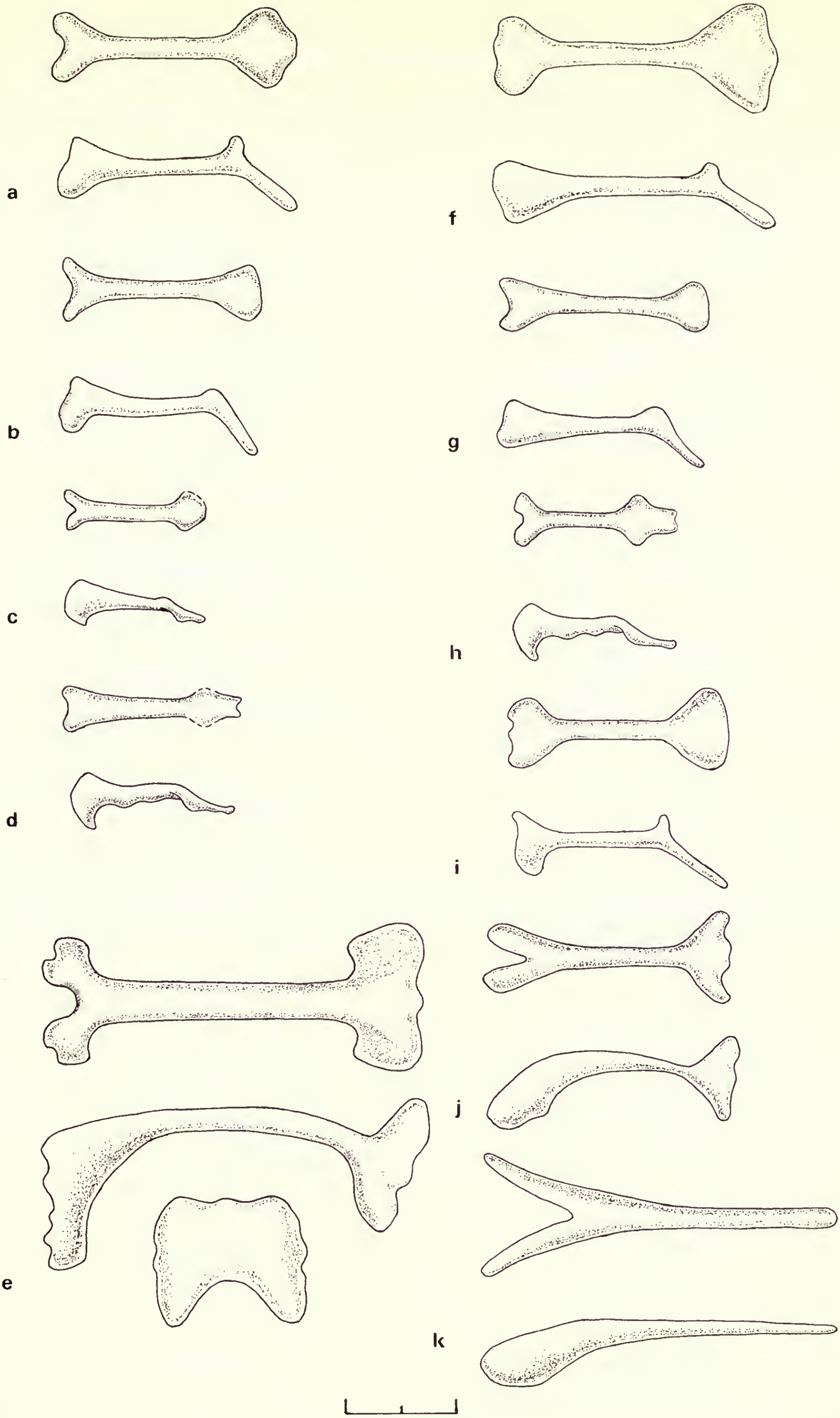

Fig. 12 Baculum (D, RL) of a, *Pipistrellus capensis* (*matroka*); b, *P. capensis*; c, *P. guineensis*; d, *P. zuluensis*; e, *P. rendalli* (with anterior view); f, *P. melckorum*; g, *P. capensis*; h, *P. somalicus*; i, *P. capensis* (*'minutus'*); j, *P. tenuipinnis*; k, *P. pumilus*. Scale = 1 mm.

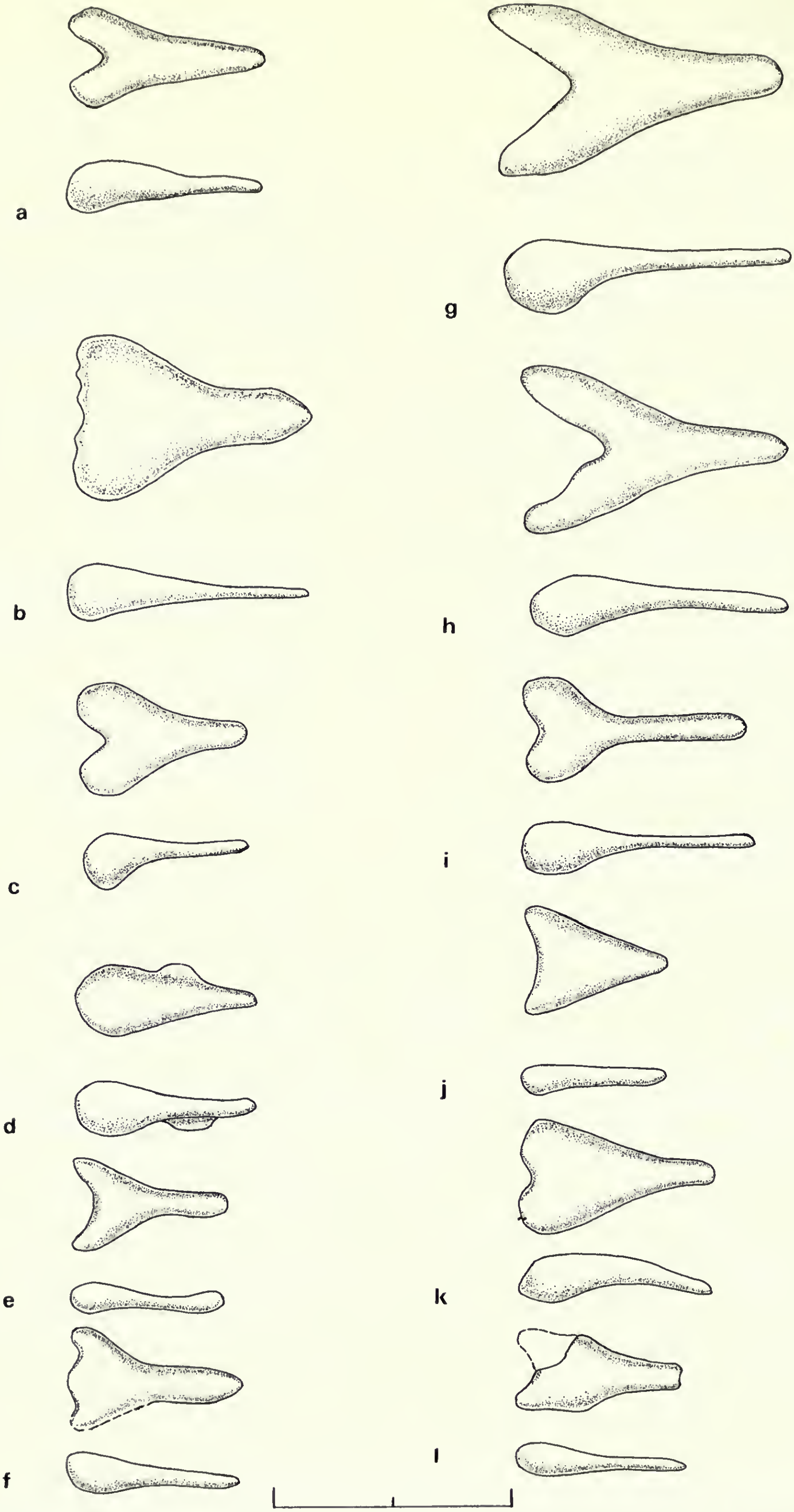

Fig. 13 Baculum (D, RL) of a, *Eptesicus fuscus*; b, *E. hottentotus* (*megalurus*); c, *E. furinalis*; d, *E. brasiliensis* (*andinus*); e, *E. bobrinskoi*; f, *E. floweri*; g, *E. serotinus*; h, *E. serotinus* (*isabellinus*); i, *E. fuscus* (*hispaniolae*); j, *E. bottae* (*innesi*); k, *E. brasiliensis*: l, *E. floweri* (*lowei*). Scale = 1 mm.

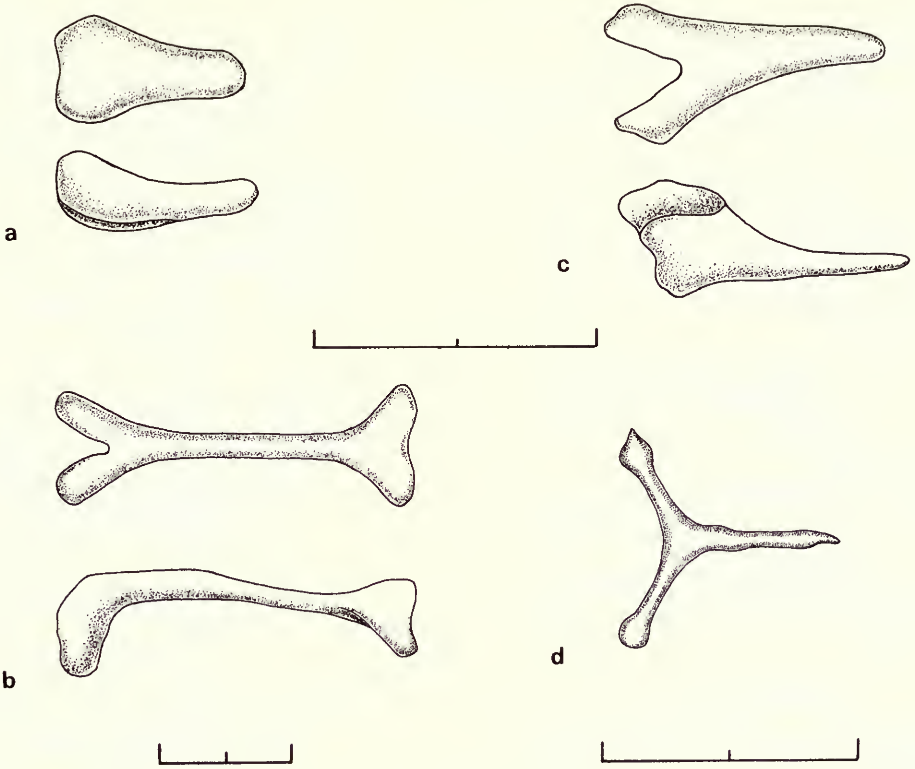

Fig. 14 Baculum (D, RL except where stated) of a, *Eptesicus bottae* (*omanensis*); b, *Pipistrellus rendalli* (? *brunneus*); c, *Eptesicus nasutus*; d, *Plecotus teneriffae* (D) (from Ibanez & Fernandez, 1986). Scales = 1 mm.

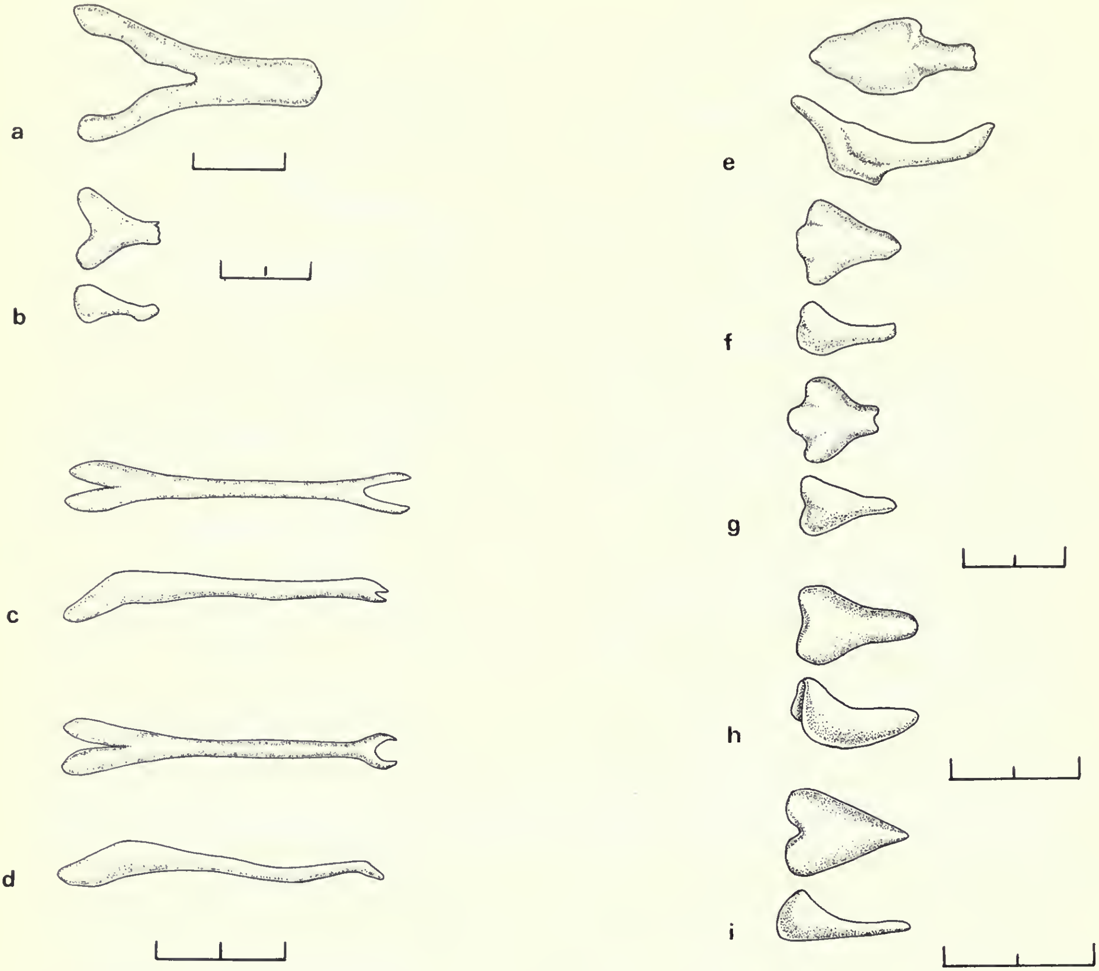

Fig. 15 Baculum (D, RL except where stated) of a, *Eptesicus nilssonii* (D) (from Topal, 1958); b, *Baeodon alleni* (from Brown *et al.*, 1971); c, *Pipistrellus peguensis* (from Sinha, 1969); d, *P. camortae*; e, *Idionycteris phyllotis*, f, *Plecotus townsendii* (*pallescens*), g, *P. rafinesquii* (e–g from Nader & Hoffmeister, 1983; h, *P. rafinesquii* (*macrotis*) (from Hamilton, 1949); i, *Bauerus dubiaquercus* (from Pine *et al.*, 1971). Scales a = 0·5 mm; b, e–i = 1 mm; c, d = 2 mm.

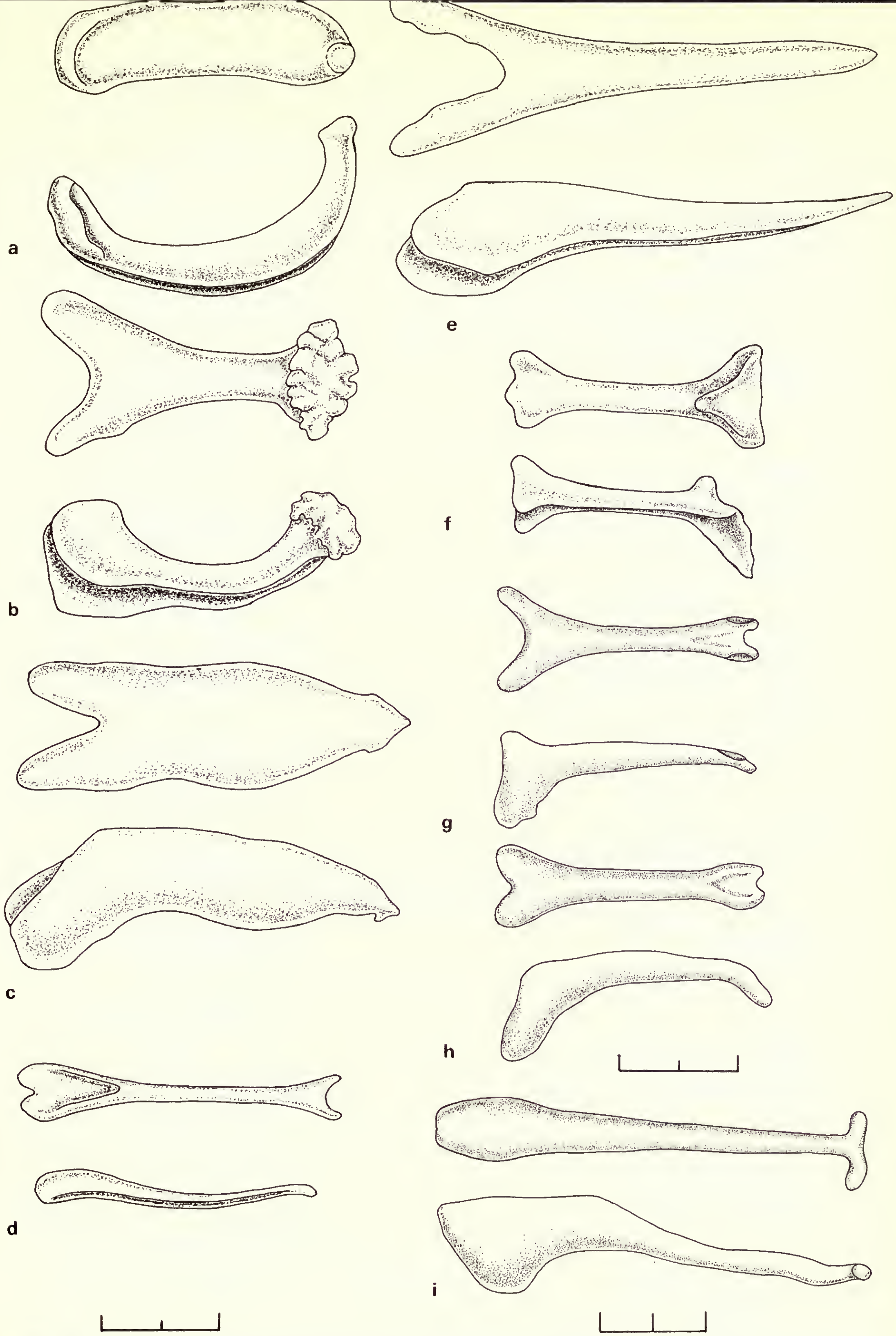

Fig. 16 Baculum (D, RL except where stated) of a, *Otonycteris hemprichii*; b, *Philetor brachypterus* (D, RVL); c, *Nyctophilus gouldi*; d, *Scotozous dormeri*; e, *Nycticeinops schlieffenii*; f, *Laephotis wintoni*; g, *Scotorepens balstoni*; h, *S. greyii*; i, *Scoteanax rueppellii*. Scales a–h = 1 mm; i = 2 mm.

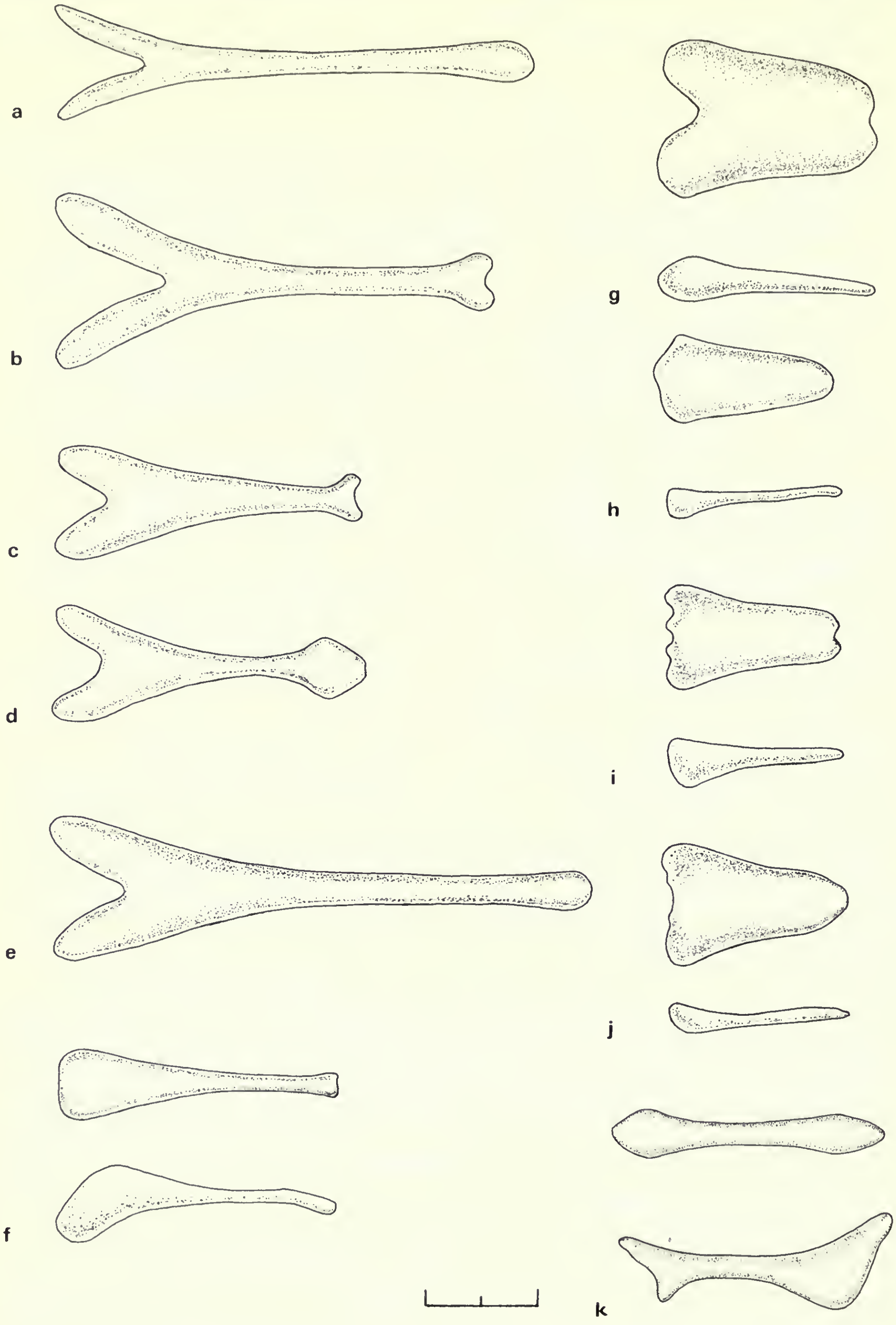

Fig. 17 Baculum of a, *Chalinolobus morio* (D); b, *C. gouldi* (D); c, *C. nigrogriseus* (*rogersi*) (D); d, *C. picatus* (D); e, *C. tuberculatus* (D); f, *Lasionycteris noctivagans* (D, RL); g, *Scotophilus nigrita* (*gigas*) (D, RL); h, *S. heathii* (D, RL); i, *S. kuhlii* (D, RL); j, *S. nigritellus* (D, RL); k, *Nycticeius humeralis* (D, LL, reversed). Scale = 1 mm.

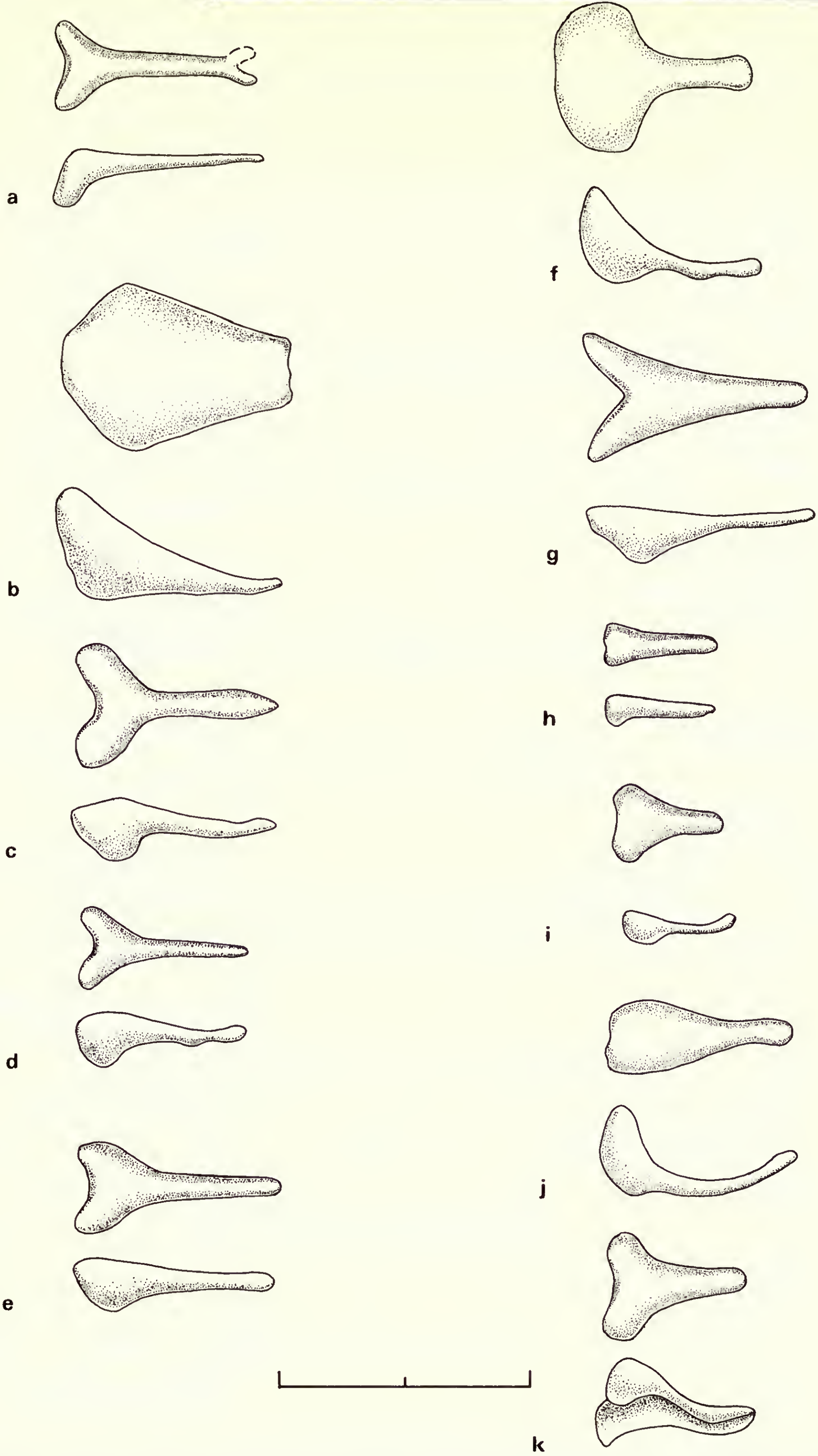

Fig. 18 Baculum (D, RL) of a, *Glischropus tylopus*; b, *Antrozous pallidus*; c, *Histiotus velatus*; d, *H.* (?) *macrotis*; e, *H. macrotis*; f, *Dasypterus argentinus*; g, *Scotomanes ornatus*; h, *Tylonycteris pachypus*; i, *T. robustula*; j, *Barbastella barbastellus*; k, *Rhogeessa tumida*. Scale = 1 mm.

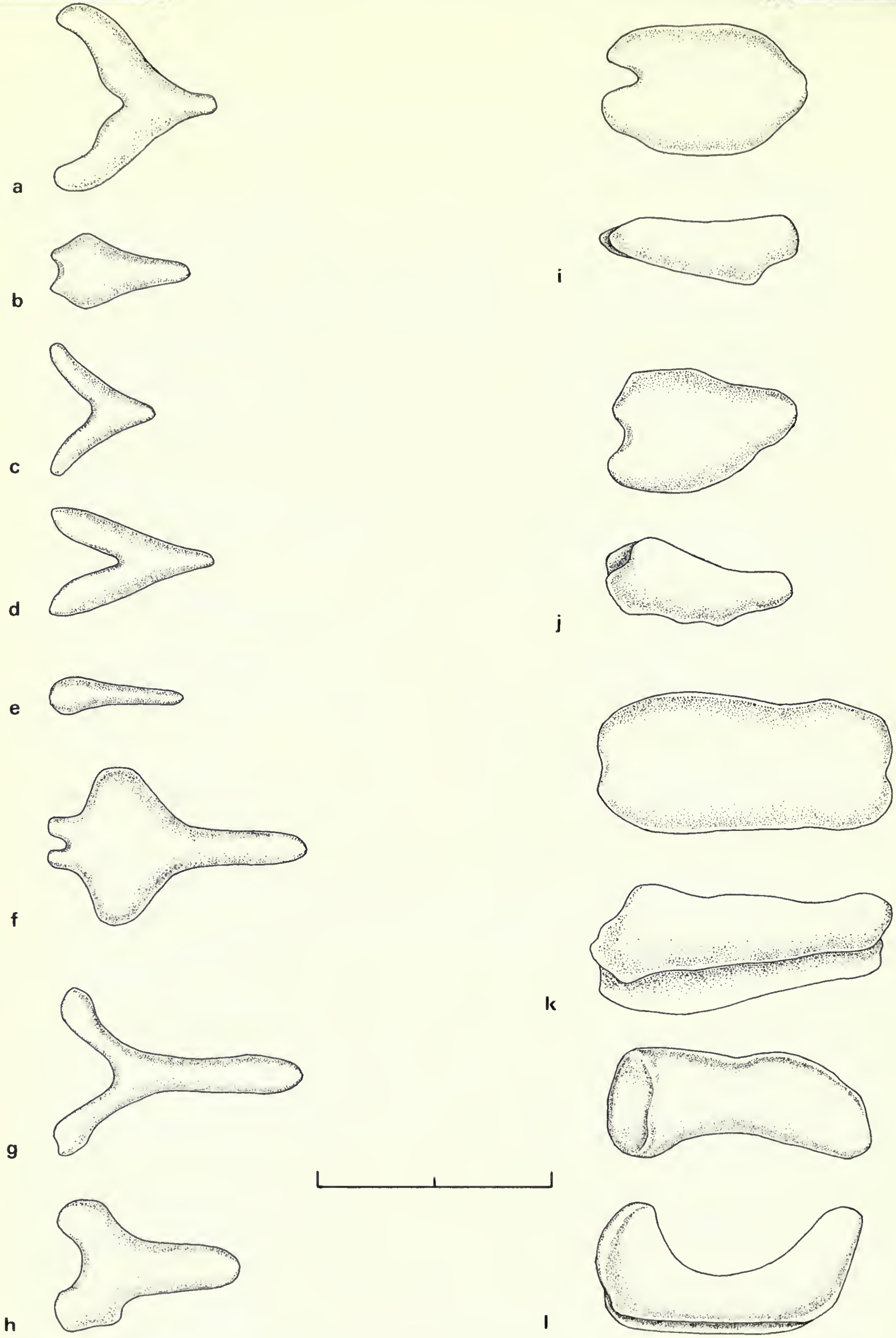

Fig. 19 Baculum of a, *Glauconycteris poensis* (D); b, *G. variegata* (D); c, *G. beatrix* (D); d, *G. argentata* (D); e, *G. humeralis* (D); f, *G. variegata* (*papilio*) (D); g, *Plecotus auritus* (D); h, *P. austriacus* (D); i, *Myotis ridleyi* (D, RL); j, *M. nattereri* (D, RL); k, *Pizonyx vivesi* (D, RVL); l, *Lasiurus cinereus* (D, RVL). Scale = 1 mm.

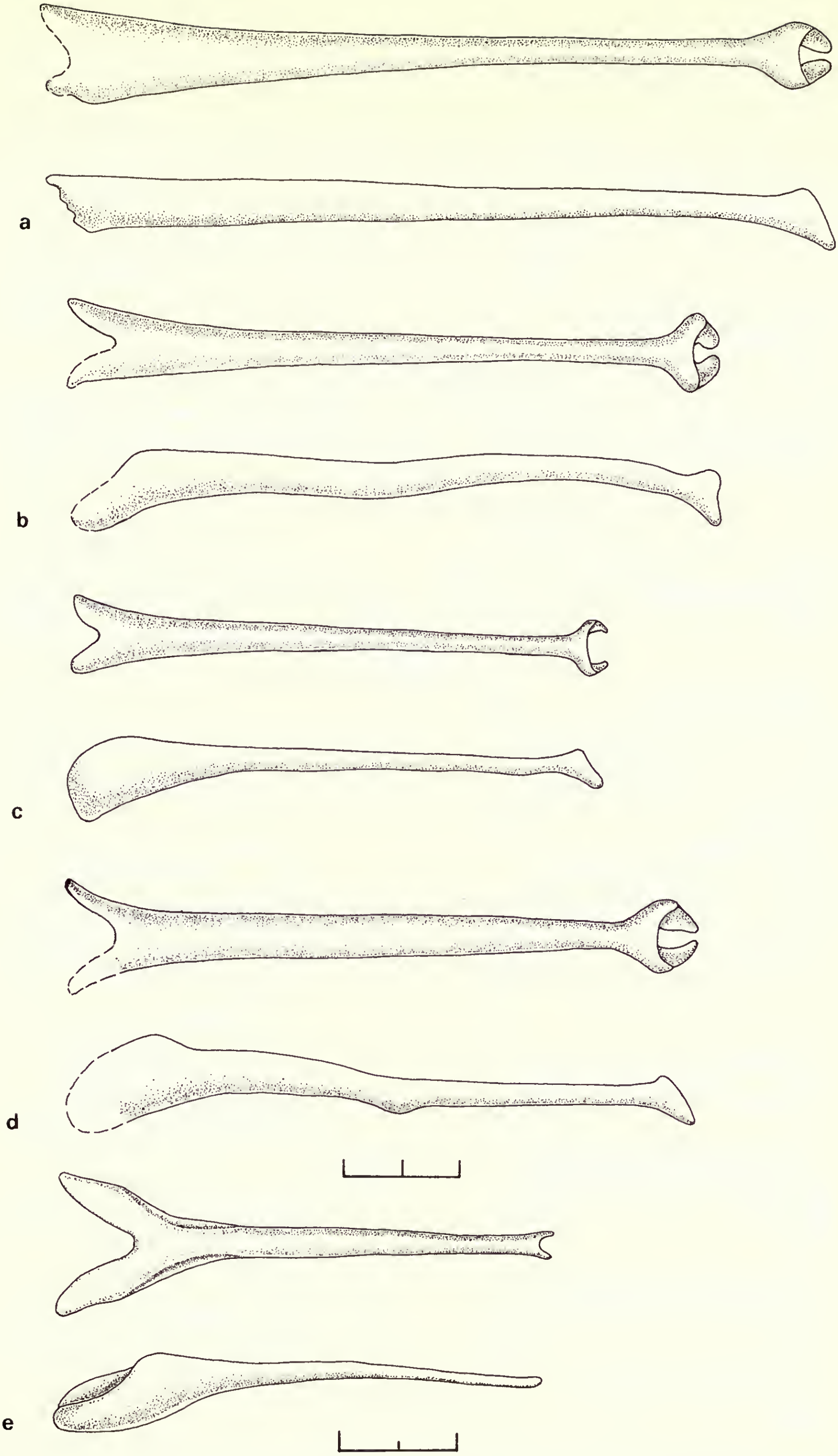

Fig. 20 Baculum (D, RL) of a, *Scotoecus albigula*; b, *S. hindei* (*falabae*) c, *S. hirundo*; d, *S. hindei*; e, *S. albofuscus*. Scales a–d = 2 mm; e = 1 mm.

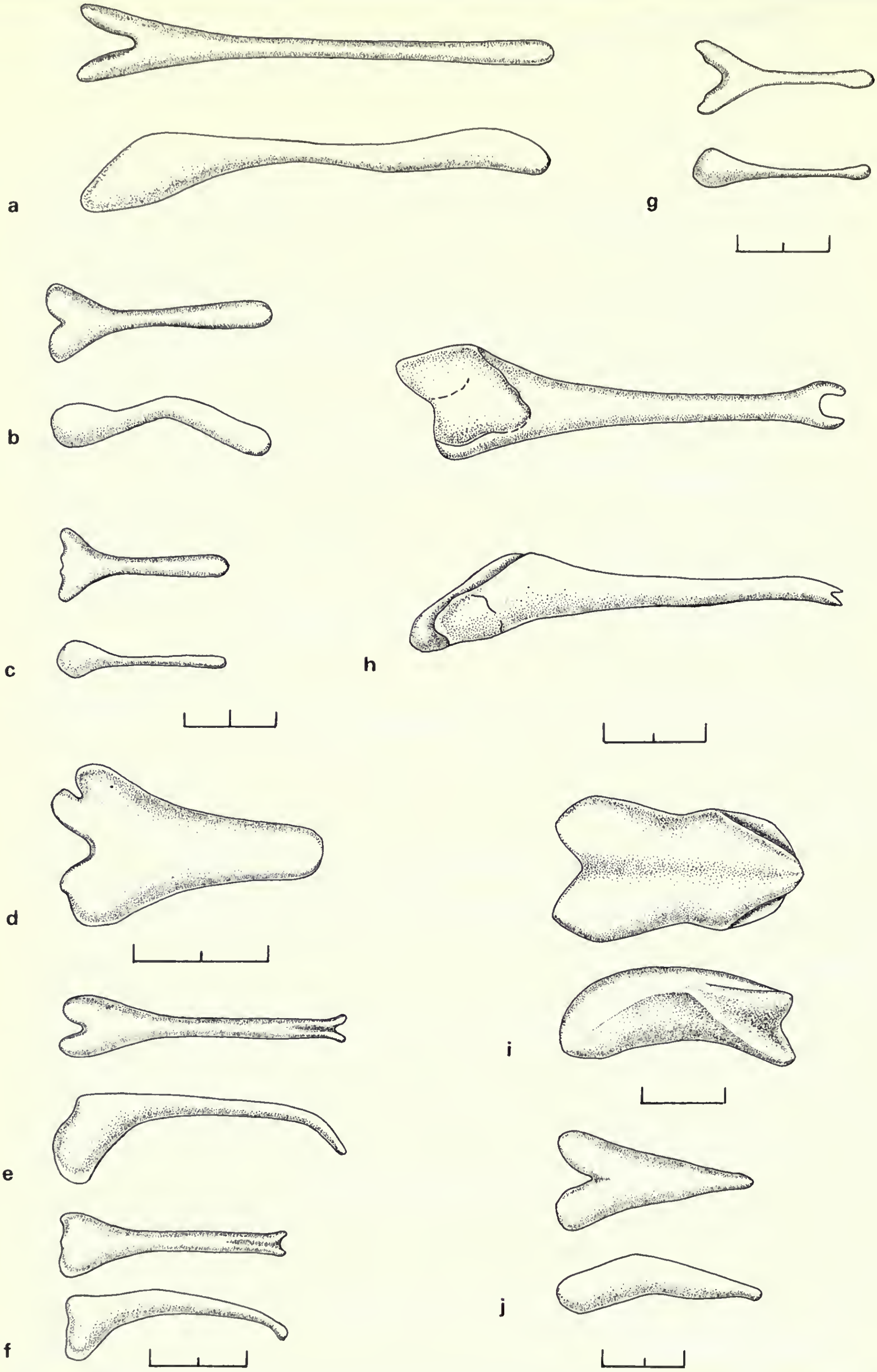

Fig. 21 Baculum (D, RL except where stated) of a, *Hesperoptenus tomesi,* b, *H. tickelli,* c, *H. doriae* (a–c from Hill, 1976); d, *Ia io* (D) (from Topal, 1970); e, *Scotorepens orion,* f, *S. sanborni* (e, f from Kitchener & Caputi, 1985); g, *Hesperoptenus blanfordi* (from Hill & Francis, 1984); h, *Scotoecus pallidus* (from Agrawal & Sinha, 1973); i, *Vespertilio murinus* (V, RL) (from Topal, 1958); j, *V. orientalis* (from Wallin, 1969). Scales a–c = 2 mm; d–h, j = 1 mm; i = 0·5 mm.

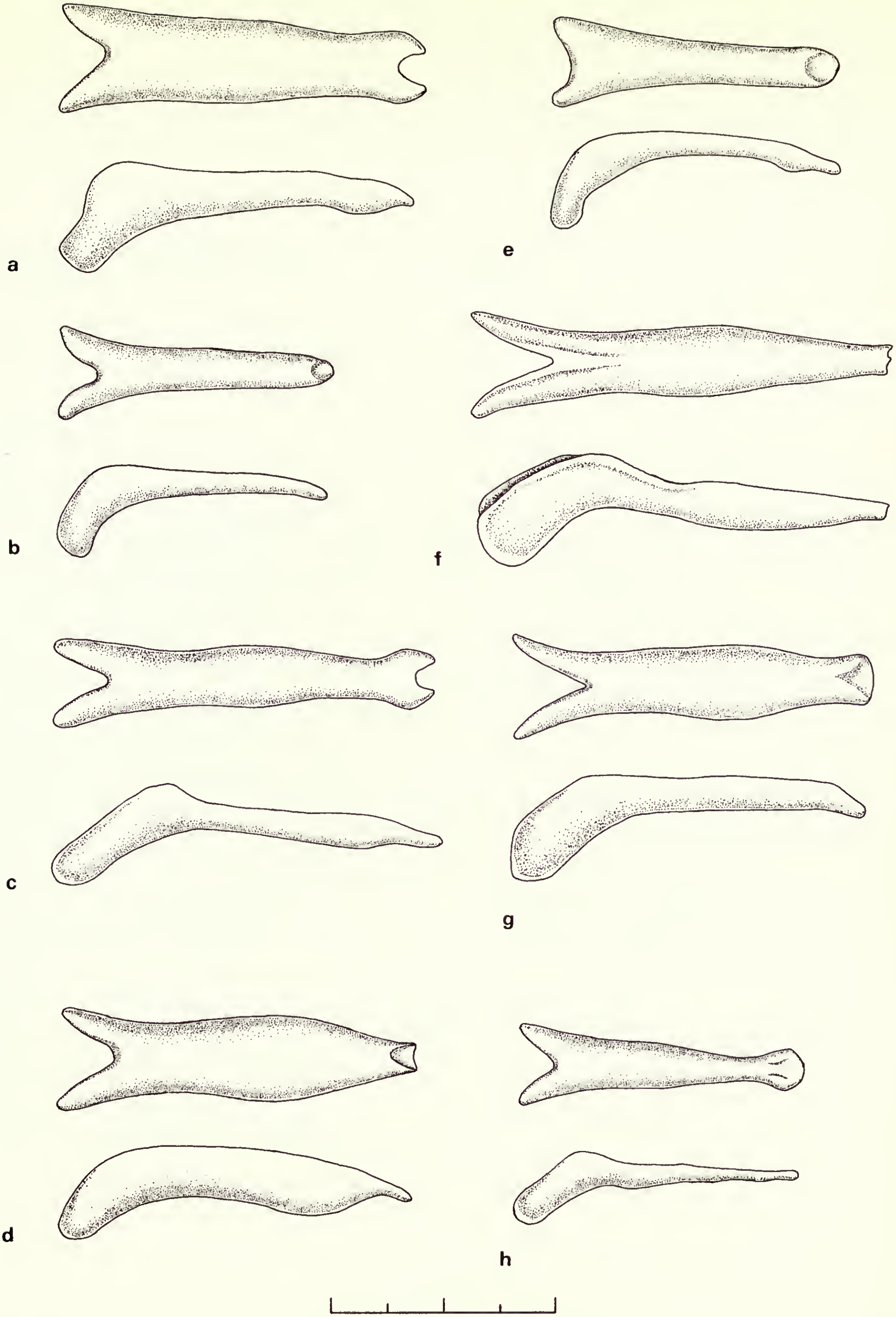

Fig. 22 Baculum (D, RL) of a, *Nyctophilus bifax*; b, *N. geoffroyi* (*pallescens*); c, *N. microtis*; d, *N. gouldi*; e, *N. geoffroyi* (*pacificus*); f, *N. gouldi* (*sherrini*); g, *N. daedalus*; h, *Pharotis imogene*. Scale = 2 mm.

British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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P. J. Chimonides

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Notes on some species of the genus Amathia (Bryozoa, Ctenostomata)

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Synopsis

The species of the genus *Amathia* have presented difficulties of recognition for a long time. Even the most recent revisionary accounts have failed to establish the separate identity of many of the species; these have, instead, been submerged in erroneous synonymies. Fifteen species are dealt with in full. In the main, species without significant spiralling of the autozooid groups are considered. Three new species are introduced: *A. guernseii*, *A. intermedis* and *A. tricornis*. A fourth species, *A. populea* Busk MS in d'Hondt, is recognised as new. *A. distans var aegyptana* is raised to specific rank. *A. cornuta* Lamouroux (preocc.) is renamed *A. lamourouxi*. *A. obliqua* and *A. plumosa* MacGillivray are redescribed. *A. alternata* Lamx., *A. biseriata* Krauss, *A. brongniartii* Kirkpatrick, *A. lendigera* Linn., *A. pruvoti* Calvet, *A. pinnata* and *A. wilsoni* Kirkpatrick, *A. woodsii* Goldstein, are redefined with type material selected. Characters for use in taxonomic and systematic discrimination are introduced, and brief comment is made on the zoo- and palaeo-geography of the species dealt with.

Introduction

The genus *Amathia* was erected in 1812 by J. V. F. Lamouroux, consequential to the study of material collected from Tasmania and the south coast of Australia by C. A. Lesueur and F. Peron, during the years 1800–1804 (Tenison Woods 1880, d'Hondt 1979).

However, *Sertularia lendigera* of Ellis (1755) from European waters became the type species of the genus, by virtue of being Lamouroux's sole mentioned species at the introduction of the genus (I.C.Z.N. article 69(d)). The species itself was validated with the publication of the 10th edition of the *Systema Naturae* by Linneaus in 1758 (and is therefore technically that of Linneaus).

Ryland (1982) gave a revised perspective classification of the genus but there are differences between his definitions of higher categories, including *Amathia*, and the characters of the genus presented here. At the Family level, Ryland described the 'zooids' as being 'radially symmetrical, no face being partly membranous'; and at the Superfamily level, he described 'branching being irregular'. Both descriptions are inaccurate for *Amathia*. Similarly d'Hondt (1983) for the Family level, also described 'External autozoecial symmetry' as 'radiated', while at the Superfamily level, there was some ambiguity in the definitions of the characteristics employed e.g. for the 'Zoarium . . . autozoecia unconnected to their neighbours'. Clearly there is need for a review of the characters

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used in the definition of the higher taxonomic levels, although this is beyond the scope of this account.

The persistent problem has been how to differentiate between the numerous species. The brief descriptions often given are of little help, and in fact have led to some confusion. Often, widespread geographical distributions have been suggested. Where no figures or specimens are available, it is unlikely that the true identity of some species will ever be recognised. Despite the efforts of d'Hondt (1979, 1983) the picture still remains clouded.

This account attempts to establish criteria for species differentiation within the genus; to identify some species groupings based upon these criteria and in the process to discuss and correct past misconceptions.

In general, the species of *Amathia* may be assigned to either of two groupings: those with autozooids spirally disposed about the stolon; those with autozooids disposed linearly along the stolon. It is mainly the latter group which is discussed here. Where spirally disposed species are dealt with, this is mainly to obviate possible confusion with those species (i.e. *A. alternata* and *A. pruvoti*) in which marked twisting of the autozooid groups occurs along the stolon. It is in the context of comparison with *A. pruvoti* that *A. distans var aegyptana* is considered.

Definition and Assessment of Taxonomic Characters

Waters (1910) in his brief account of the genus, outlined a number of characters which may serve as a foundation on which to build an understanding of both the genus and its species. These characteristics may be added to, and arranged in what is considered here to be an order of decreasing reliability, reflecting an increase in their intraspecific variability.

List of species discrimination characteristics in order of reliability

(1) budding pattern of stolons
(2) development of any kenozooidal processes or rhizoids and their orientations
(3) arrangement of autozooids about the stolons
(4) autozooidal thickening
(5) profile of autozooids and stolons
(6) number of autozooids and proportion of stolon occupied by autozooids
(7) dimensions of components

The potentially informative characters of larval type, larval metamorphosis, ancestrula formation and initial colony development are generally not known and hence cannot be evaluated. Despite the explicit account given by Barrois (1877) for *A. lendigera*, the ancestrula and earliest astogenetic stages, for example, have not been recognised in any of the specimens examined. In some specimens it was clear that this part of the colony was absent; in others, it was impossible to see because of heavy overgrowth by the colony's own rhizoids or by spatial competitors. For these same reasons, in the following systematic accounts, no information is given on the non-erect part of the colony for the majority of species. It is possible that some colonies are the result of association between the products of more than one ancestrula, (without the necessity for fusion to have occurred, especially in the non-arborescent growth forms). Zimmer and Woollacott (1977a) suggested that the larval type of all stoloniferan ctenostomes is the same. It would appear however, that their conclusions were drawn from only three species: '*Amathia lendigera*', *Bowerbankia pustulosa* (Ellis and Solander) and *Zoobotryon verticillatum* (Delle Chiaje). Furthermore, Zimmer and Woollacott (1977*b*) pointed out that past accounts of metamorphosis of larvae in this group were inconsistent, and that 'additional work is essential to clarify the pattern(s) of metamorphosis' of the larval type. Waters' (1910) intuitive suggestion of the 'valuable assistance' which the primary zooecia might give must, therefore, be discounted for the present.

Extensive examination of several large colonies indicates that the branching pattern of stolons remains remarkably consistent within species. Differences in branching pattern may be inferred to have been microenvironmentally induced in that they tend to be sporadic, involve the development of new stolens from astogenetically early regions of the colony, and are often associated with the presence of epibionts. The budding patterns, together with kenozooidal processes, rhizoids, autozooidal thickenings and disposal of autozooids about the stolons, can give rise to characteristic colony shapes which, with familiarisation, allow identification of species by casual inspection.

The growth of a colony relies essentially on the production of the supporting 'stolonal' kenozooids. Where such a kenozooid is destined to bear autozooids, the autozooids are usually seen to develop at about the same time as the kenozooid lengthens through apical growth. Autozooid-bearing kenozooids are here termed stolons. The position of the autozooids and the proportion of stolon occupied by them is highly regular. Stolonal and autozooidal growth is considered to have ceased with the production of septa at the distal end of the stolon, and the subsequent appearance of daughter stolonal buds. The kenozooidal processes of character No. 2 in the above list appear to be growth-terminating features. These are usually distinguishable from potential autozooid-bearing stolonal kenozooids by being straighter, narrower, often tapering to a point, and frequently being subdivided by septa.

Where rhizoids are to be produced by a structure, the origin of each rhizoid is marked first by the appearance of an oval window in the cuticle. Rhizoids then develop as papilliform outgrowths of these windows, proximally directed along the colony, growing towards the colony base. The rhizoids sometimes fuse with each other en route, overgrowing and obscuring underlying stolons, and forming a trunk-like mass. Autozooids and lateral branches of overgrown stolons are often shed. When rhizoids are produced, the resulting colony form is usually arborescent.

The overall cuticular thickening of any colony appears uniform, except at the regions of the growing tips, where it is thinner. This level of cuticular thickening can differ between colonies of the same species. As this thickening is contributory to colour, it follows that colour is also variable. Within all species, there are localised areas of thickening, which tend to be constant. Thickening in the autozooids, which gives their groupings a characteristic appearance, may be used to discriminate between species. Two conditions occur: one where the walls between autozooids are differentially thickened (inner-wall thickening); the other where the outer walls are differentially thickened (outer-wall thickening) (see Fig. 1B, C).

The arrangement of autozooids on the stolon is usually described as being paired, or as a biserial row. Although this appears correct, in all specimens examined, displacement of autozooids occurs, so that the autozooids of one row interlock with the recesses between the autozooids in the other row (Dalyell, 1847 for *A. lendigera*). Very frequently, this emphasises a single proximal-most autozooid in each group. No pairing of autozooids may be confidently assigned throughout a colony in any species, and there can be odd or even numbers of autozooids in any autozooid group. In some cases, notably those with inner-wall thickening, the proximal-most autozooid tends to be larger in cross section and displaced centrally, such that it can be very difficult to assign it to a row of origin at any stage in its ontogeny.

Materials and methods

Specimens used for study were mainly those of the British Museum (Natural History), London, (BMNH) and The Manchester Museum, (MM), with additional material referred to as follows: Laboratoire de Biologie des Invertébrés Marins et Malacologie of the Muséum National d'Histoire naturelle, Paris, (LBIMM); the National Museum of Victoria, Melbourne, (NMV); the Rijksmuseum van Natuurlijke Historie, Leiden (RM); and the U.S. National Museum, Washington, (USNM).

Often, the material for study had been preserved dried, with resulting distortions. To observe the autozooidal characteristics preserved in the cuticular thickenings, it was found far better to rehydrate the specimens although it was still possible to make identifications without treatment. Rehydration was carried out using tri-sodium phosphate in 7–10% aqueous solution, with subsequent transfer to distilled water and then via a sucession of increasing concentrations of alcohol, to 80% concentration for storage. From this process, specimens regained the turgidity associated with their living state. It was from specimens in this turgid state that measurements were taken.

Some care was needed, as rupture of specimens was possible through the initial high osmotic differential established on transfer to distilled water. In some cases, specimens failed to reflate because of existing ruptures in their cuticles.

In the ensuing descriptions, anterior is used to denote the side at that location bearing autozooids, and posterior, the side opposite (see Fig. 1D, E). Dimensions are given in millimetres and are means of a minimum of 30 measurements. Where shape negated the validity of a single sample measurement, extreme dimensions are given, these also being the means of 30 measurements each. Measurements were made in ontogenetically complete components, near distal regions, avoiding where possible, astogenetically earlier (older) regions of the colony. No attempt was made to determine intra-colony variations quantitatively. Where these were noted, they were assessed subjectively.

The following abbreviations are used:

Sl.	length of stolon
Sd.	diameter of stolon, at location specified; usually midway along the proximal autozooid-free end.
Zh.	autozooid height to the highest point on the rim of thickening, of tallest autozooids, unless otherwise specified.
Zw.	autozooid width, measured along the stolonal axis.
Z/S.	the linear proportion of stolon occupied by autozooids
Zn.	the number of autozooids per autozooid group (and apparent number of 'pairs')
Tpl.	length of terminal process

Key to species

(Identification is best attempted with plentiful material.)

1	Rhizoids developed, colony frequently aborescent	2
–	Rhizoids not developed, colony not arboresecent, no terminal processes and Z/S ratio <50%	13
2	Autozooidal thickening inner-wall	***brongniartii***
–	Autozooidal thickening outer-wall	3
3	Branching nearly always bifurcate	4
–	Branching primarily tri- and tetrafurcate, bifurcation may also be present	10
4	Terminal processes developed	5
–	Terminal processes not developed	7
5	A pair of lanceolate, single-kenozooidal terminal processes developed at the distal end of each autozooid group, arising in the same direction as the autozooids	***lamourouxi***
–	Lanceolate terminal processes of compound kenozooidal construction, each filament developed in place of a normal stolon, sometimes branched	6
6	Rhizoids developed postero-laterally, terminal processes never branched	***populea***
–	Rhizoids developed anteriorly, terminal processes often forked	***woodsii***
7	Autozooids re-orientated by approx. 180 deg. from stolon to stolon, polyrhizoidy (see page 335) possible	***alternata***
–	Autozooid orientation from stolon to stolon maintained within 30 deg., rhizoids paired at most	8
8	Rhizoids developed anteriorly, autozooids with marked distal inclination, autozooid group profile diminishing distally	***guernseii***
–	Rhizoids developed postero-laterally, autozooid group profile horizontally even i.e. level	9
9	Stolons curved anteriorly, curvature increasing distally, autozooid group arranged in line with stolonal axis	***biseriata***
–	Stolons straight, autozooid group set obliquely to stolonal axis	***obliqua***
10	Autozooid-bearing stolons developed laterally from a central axis of stolon-sized, or larger, kenozooids. Autozooid-bearing stolon sequences end with compound terminal processes, these often forked	***plumosa***
–	Autozooid-bearing stolons developed laterally from a central axis of other autozooid bearing stolons	11

11 Central axis stolons undergo trifurcation only; indistinguishable from lateral stolons . ***pinnata***

– Central axis stolons usually undergo tetrafurcation, a fourth autozooid-bearing stolon developed posteriorly. Central axis stolons morphologically distinguishable from lateral stolons, differences may be slight 12

12 Autozooid-bearing stolon sequences end with lanceolate, compound kenozooidal, terminal processes, each replacing a normal stolon and thus in complements of three. Pronounced difference between central axis and lateral stolons. . . . . ***tricornis***

– Autozooid-bearing stolon sequences with pinnate, compound terminal processes; each assemblage replacing stolons in other, regular positions, giving characteristic arched colony sub units. Difference between central axis and lateral stolons slight . . . . . . ***wilsoni***

13 Autozooid groups regularly twisted along stolon length . . . . ***pruvoti***

– Autozooid groups rarely showing any twist 14

14 Stolons often in rectilinear series, straight, sometimes undergoing trifurcation. Autozooid groups often remote from subsequent branching point. Autozooids usually erect . . ***intermedis***

– Stolons of variable length, usually short, sculptured and posteriorly deflected. Autozooid groups overlie subsequent branching point, autozooids inclined distally, the lean increasing distally . . . . ***lendigera***

Systematic Section

Phylum **BRYOZOA** Ehrenberg, 1831
Class **GYMNOLAEMATA** Allman, 1856
Order **CTENOSTOMATA** Busk, 1852
Genus ***AMATHIA*** Lamouroux, 1812: p. 184

Part *Sertularia* Linnaeus, 1758.
Serialaria Lamarck, 1816.
Part *Valkeria* Dalyell, 1847.
Amathella Gray, 1858.
Charadella Gray, 1858.
Serialia Gray, 1858. (errorum pro *Serialaria* Lamarck, 1816).
Spiralia Gray, 1858.
Cornalia Gray, 1858.
Amathia: Bobin & Prenant, 1956: (incomplete cum. syn., NB. Gray 1858 misquoted as 1848); Ryland, 1982; Winston, 1982; d'Hondt, 1979, 1983; Hayward, 1985.

TYPE SPECIES. *A. lendigera* (Linnaeus 1758 *sensu* Ellis 1755) Lamouroux 1812: p.184.

GENERIC DESCRIPTION. Colonies mainly erect with a creeping base, this sometimes extensive. Autozooid groups displaced towards the distal portion of the stolon. Stolons may produce rhizoids, proximally disposed. Distal, mainly growth-terminating kenozooidal processes may be developed from various positions. Autozooids with gizzards, borne on kenozooidal stolons, arising from rosette plates, in groups, connate for at least part of their length, appearing biserially arranged as a straight or spiral series.

REMARKS. The only attempt to regroup species comprising the genus *Amathia* was made by Gray (1858, duplicated 1859). Gray introduced several indeterminate subgeneric or generic groups, the type species of which were insufficiently described and not illustrated. The great majority of the limited characteristics employed are variable within species, such that none of the divisions Gray introduced exclusively defines any species group identifiable within the genus. Bobin & Prenant (1956) are followed here in assigning all species described to the genus *Amathia*.

Amathia lendigera (Linnaeus, 1758)
(Figs 6A, 7A)

? *Sertularia lendigera* Ellis, 1755: 27, pl. 15 (figs 24B, 24b).
Sertularia lendigera Linnaeus, 1758: 812.
Amathia lendigera Lamouroux, 1812: 184.
Not *Amathia lendigera*: MacGillivray, 1895: 135, pl. B (fig. 1).
Not *Amathia lendigera*: O'Donoghue & de Watteville, 1944: 430 (= *A. populea*).
Part *Amathia lendigera*: Bobin & Prenant, 1956: 280.
Amathia lendigera: Hayward, 1985: 134, fig. 45B.

MATERIAL EXAMINED

Neotype (selected here): BMNH; 1963.1.8.3, Chichester Harbour, H. G. Stubbings collected.

OTHER MATERIAL

BMNH; 1827.11.18.8, no locality. 1852.3.16.62, Weymouth. 1882.7.7.85, no locality. 1887.7.23.5, Solent, I.o.Wight. 1891.8.7.18, Portland, Dorset. 1897.8.9.67, Weymouth Bay, Portland, 10 fthms. (18.29 m). 1899.5.1.211, ?Off Saints Bay, Guernsey? 1900.10.30.10–11, Weymouth. 1912.12.21.681, Plymouth.

MM; 7093–4, Naples. 7095, Roscoff, France. 7096–9, Swanage. 7105, Naples. 7106, St. Raphael, S. France. 7107, Rapallo (=Rapolla, Italy?).

DESCRIPTION. Colonies tend to have to have a moderately extensive creeping component of stolonal kenozooids. These are adpressed to the substratum and closely follow its profile, showing reduced branching in some places and multiple branching in others. These stolonal kenozooids are usually of irregular form and length, and only rarely bear autozooids. Bilateral palmate processes are often produced, through which adhesion to the substratum is effected. Erect components may be produced at any branching point, with or without continuation of the creeping component. The erect components develop as the characteristic autozooid-bearing stolons, arranged in the typical form of an orbicular mass, cotton-wool like in appearance, utilizing well the available free space near to the substratum. These erect components appear tangled, but are rarely so. Any erect component may resume the creeping habit on contact with the substratum. Branching in the erect part of the colony is practically always bifurcate, ranging from equally dichotomous to almost rectilinear with side branches, these appearing on alternate sides. Bifurcations typically form an angle of 90 deg. Autozooid group orientation about the stolon is not usually preserved from stolon to stolon. Daughter stolons often arise deflected anteriorly to maternal stolons. Autozooid groups, with relatively few autozooids, occurring at the extreme distal end of stolons, frequently overlapping the subsequent branching point. Stolons are often deflected posteriorly at the proximal end of the autozooid group, and also raised slightly on the anterior surface at this same region. Stolons may be of variable length. Autozooids are outer-wall thickened. Autozooid profile diminishes distally, due in part to decreasing autozooid height, and in part to increasing distal inclination of the autozooids. A proximal-most autozooid is usually prominent in each group and is displaced centrally. Where not truly central, this autozooid remains on the same side of its stolon as the direction in which that stolon was budded. The arrangements of autozooids on sister stolons are therefore mirror images of each other (see Fig. 5B). Where stolons form linear sequences, autozooid groups borne on such series tend to show an alternate sequence of autozooid displacements on successive stolons. Sometimes sister stolons carry identical autozooid displacements, these being opposite to that on their maternal stolon. No overall pattern is discernible within the colony in the occurrence of this second state of succession (see Fig. 5C). Rhizoids are absent.

Sl. 1.25–2.75
Sd. 0.75–0.97
Zh. 0.33–0.50
Zw. 0.10–0.12
Z/S. 25–50%
Zn. 8–17 (appearing as 4–8 'pairs')

REMARKS. According to Harmer (1931), the original specimens described and figured by Ellis (1755) were not kept (I.C.Z.N. article 73(b) (i), recommendation 69B). Harmer stated that specimens of *A. lendigera* were sent to Linnaeus by Ellis, but some 12 years after the publication of the nomenclaturally significant 10th edition of Linnaeus' *Systema Naturae* (1758). Two specimens, under the original name of *Sertularia lendigera*, are still in the collections of the Linnean Society of London (Nos. 1298.17 and 1298.18). The specimens are preserved pressed dry on paper, and both are labelled as 'lendigera' in Linnaeus' handwriting. From examination of these specimens, some doubt arises that Ellis and Linnaeus were sufficiently rigid in their interpretation of *A. lendigera*. Two species are present: specimen 1298.17 is identifiable as *A. semiconvoluta* (see pages 335, 338); while specimen 1298.18 is probably *A. lendigera*. Linnaeus (1758) has trustingly used Ellis' (1755) description verbatim. If the specimens originated from Ellis, Linnaeus may also have accepted their identity from him. It is possible therefore, that the mistaken identity of 1298.17 could be attributed to Ellis; neither man realising the presence of mixed material.

However, there is some evidence in support of Harmer's statement that the Linnaean specimens are not Ellis' original (1755) material. Linnaeus is reported to have been in the habit of upgrading his botanical collections, with the replacement of older specimens by new, 'some of them not conspecific by modern taxonomic standards' (Stearn, 1957), a practice which could also have been applied to herbarium preparations of 'zoophytes'. In addition, none of the figures of Ellis (1755) correspond with either of the Linnean Society specimens, in particular specimen 1298.18. Features of importance are: the arborescent and open appearance of the colony shape in figure '24b'; the number of autozooids per stolon indicated by the magnified view in figure '24B'. Although only a single line of autozooids is drawn in the latter figure, this may be interpreted as showing either: a single proximal-most autozooid with indications of the outlines of subsequent 'paired' autozooids; or possibly a line of 'all paired' autozooids. The condition depicted is readily seen in many dry preserved specimens, where only the thickened outer walls, forming the periphery, survive well. As such, 17 or 18 autozooids would be represented on three of the five stolons; 15 autozooids would be represented on one of the remaining two; and there is an inexplicable absence of autozooids on the remaining fifth and final stolon. Although notionally possible, it is very unusual for *A. lendigera* to show as many autozooids per stolon in direct succession in a colony. The importance of this analysis is that figure '24B' is claimed as an exact microscope drawing.

Harmer (1931) suggested that figures of Ellis be regarded as the lectotype of the species. However, the figures are inadequate, no rhizoids are shown, and their presence or absence is not indicated in the description. On the cumulative evidence (see above), figures '24b' and '24B' could thus be depictions of *A. intermedis* or even *A. guernseii.*

Selection of a neotype specimen is the only satisfactory way to resolve the identity of *A. lendigera*; particularly important as the species is the type of the genus. There is no indication that the Linnean Society specimen 1298.18 formed any basis for the description for the species. In addition to the uncertainties surrounding its status, 1298.18 unfortunately also lacks sufficient locality data, is not in an adequate state of preservation, and so should not be considered. Specimen BMNH 1963.1.8.3 is therefore selected here as neotype. It is preserved in alcohol, growing on *Halidrys siliquosa* as is the Linnean Society specimen. BMNH 1963.1.8.3 is erroneously listed by d'Hondt (1983) as *A. pruvoti*, a very different species (see pages 336, 337).

There is great similarity between *A. lendigera* and *A. intermedis* and both resemble *A. guernseii* (see pages 316, 317). The morphologies of all three may overlap in different parts of the colony. *A. lendigera* differs from *A. intermedis* in that: it tends to have fewer autozooids per autozooid group; the autozooids have an increased distal inclination; the autozooid group profile diminishes distally more rapidly; the autozooid groups and subsequent bifurcation sites are more condensed relative to each other; it has a more compact colony form, with low incidence of rectilinear succession. Great care is needed to distinguish between the trifurcation that may occur in the erect part of the colony of *A. intermedis*, and the multiple branching, including trifurcation, which occurs in the immediate vicinity of the non-erect part of *A. lendigera*, as detachment from the substratum is frequent in preserved specimens. Non-erect stolons may usually be identified by the nearby presence of palmate processes (see Fig. 8A), and the irregular morphology associated with the creeping mode.

The displacement of the proximal-most autozooids in maternal and daughter stolons, may reflect the timing of the production of daughter stolons relative to each other. The mirror image arrangement (see Fig. 5B) possibly results from the simultaneous production of the daughters.

Most of the published records for *A. lendigera* are listed in a lengthy synonymy by Bobin and Prenant (1956). However, many of these records are unsupported by specimens available for examination and are thus equivocal. In addition, the account these authors give mentions the occurrence of rhizoids, and thus includes another species, probably *A. guernseii.*

Three specimens in the Waters Collection in the MM. (7100, 7101, 7102) from Zanzibar, are superficially similar to *A. lendigera*. However, notwithstanding the little material present, it is possible to see that the autozooid groups lack any characteristic distal inclination. In addition, the linearly disposed stolons seem to be arranged in true rectilinear fashion and lack any posterior deflection associated with stolons of their length as in *A. lendigera*. Another specimen (7104) from Menton (southern France) labelled 'A. lendigera', shows trifurcation at four stolons in almost direct succession, but conforms in most other characteristics. These stolons are all in proximity to substratum attachment sites and are probably not typical of the whole colony budding pattern. These is not enough material to be certain about this or the true identity of the specimen. The locality is, however, within the expected distribution area of *A. lendigera*. Some of MacGillivray's specimens (NMV 65387–8) marked 'British', are *A. lendigera*. Additional material (NMV 65383–5) labelled 'A. lendigera' and from Western Port, Australia, is a different species. These specimens bear little resemblance to the 'British' material, and in addition, show evidence of rhizoids. Where the rhizoids are not obvious, careful illumination is required to observe the oval window precursors. The specimens are probably early astogenetic stages of *A. lamourouxi*, but there is not enough material to be certain; the characteristic terminal processes are not present, and the identity is inferred from the branching characteristics. The 'Australian' specimens may be the material described as *A. lendigera* by MacGillivray (1895, pl. B, fig. 1), although the actual specimen figured does not appear to have been recorded.

DISTRIBUTION. *A. lendigera* is known from the Thames estuary, and along the south and west coasts of England. The species also occurs off the north coast of Africa, off Mediterranean southern France, and Naples and 'Rapallo' in Italy. Substrata recorded are rocks and the alga *Halidrys siliquosa.*

Amathia intermedis sp. nov.

(Figs. 6C, 7C)

? *Serialaria lendigera*: Johnston, 1838: fig. 40.
? *Serialaria lendigera*: Johnston, 1847: fig. 68.
? *Serialaria lendigera*: Couch, 1844: pl. 16.
Valkeria lendigera Dalyell, 1847: 249, pl. 52 (fig. 2).
? Part *Amathia lendigera*: Bobin & Prenant, 1956: fig. 124, I, IV.

Holotype: BMNH; 1887.5.2.18 part, Hastings, England.

Paratypes: BMNH; 1842.12.9.14, Belfast Bay. 1847.9.24.184, North'd (=Northumberland?) Coast. 1887.5.2.18 part, Hastings. 1963.2.10.1, Scarborough. 1985.3.2.1a, 1b, Yarmouth. 1985.3.2.2, Bournemouth. 1985.3.2.3, no locality.

ETYMOLOGY. The species at one time seemed intermediate in character between *A. lendigera* and *A. guernseii.*

DESCRIPTION. In the erect part of the colony, branching is primarily bifurcate, ranging from equally dichotomous to rectilinear series with side branches. There is a disposition to the latter condition, where at a bifurcation, one daughter stolon usually remains in line with the main axis of the maternal stolon, while the other daughter stolon appears sequentially on alternate sides. These lateral daughter stolons are produced at the same distal inclination to the maternal stolon axis as the maternal stolon autozooids. Their lateral angular inclination may be from 0–90 deg. to the orientation of the maternal autozooids, but usually ranges from 10–30 deg. Occasionally there is a trifurcation, in which, of the three daughter stolons produced, the middle one lies in the rectilinear position. The other two are produced one on either side, separated from the central one by approximately 45 deg. The autozooids on the maternal stolon bisect this angle. Autozooid groups occur towards the distal end of stolons, but there is usually a further autozooid-free portion of stolon, distal to the autozooid group. This is often axially well divided into small branches, the subdivisions orientated in the same direction as, and supporting, the daughter stolons. There is frequently a further autozooid-free length between the end of the autozooid group and this region of division, approximately equal to the diameter of one autozooid. Stolons are often straight, showing little sign of accommodating the autozooids borne. The autozooids tend to be erect, and of even height throughout the autozooid group, although autozooid group profile sometimes diminishes at the distal end. This is due in part to an increased inclination in the autozooids, and in part due to decreasing autozooid height. Autozooids are outer-wall thickened, but thinly so overall, and pale yellow brown in colour. Viewed anteriorly, a proximal-most autozooid is usually evident in each autozooid group. The occurrence of this autozooid, the pattern of autozooid displacements, and the succession states of autozooid displacements on the stolons, are identical to that found in *A. lendigera* (see page 313). The orientation of the autozooid group about the stolon is not always preserved from maternal to daughter stolons; re-orientations of up to 180 deg. may occur. No rhizoids are produced, and the colony attains a diffuse cotton-wool like appearance. The non-erect part of the colony does not appear as extensive as the erect part. Stolonal kenozooids in the non-erect part of the colony: produce branches occasionally; tend not to bear autozooids; are not of the same appearance as those of the erect part, in being elongated, sometimes twisted, and generally following the profile of the substratum. Erect components may be produced at any branching point, these assuming the normal erect growth pattern. Attachment to the substratum is effected through lateral palmate processes, often developed bilaterally from the adnate stolonal kenozooids.

Sl.	1.75–3.25	Z/S.	35–50%
Sd.	0.80	Zn.	8–29 (appearing as 4–14 'pairs')
Zh.	0.35–0.45		
Zw.	0.10		

REMARKS. *A. intermedis* resembles *A. lendigera* and *A. guernseii*, the closest similarity being with the former. *A. intermedis* may be distinguished from *A. lendigera* in having the following characteristics: trifurcations in the erect part of the colony; a tendency towards higher numbers of autozooids in the autozooid groups, and longer stolons; a staggered occurrence of autozooid groups and branching sites; a more open colony form, resulting from a higher occurrence of rectilinear succession in the stolons. *A. intermedis* may be distinguished from *A. guernseii* primarily in the fact that *A. guernseii* develops rhizoids.

As with *A. lendigera*, the displacement of the proximal-most autozooids in maternal and daughter stolons may reflect the timing of the production of the daughter stolons relative to each other (see page 314).

BMNH 1842.12.9.14, 1847.9.24.184, from Johnston's collection, are *A. intermedis*, but it is not known if any of this is his figured material (1838, fig. 40, 1847, fig 68).

DISTRIBUTION. The species is known from the east and south-eastern coasts of England, and also from Belfast Bay. The only substratum recorded is the alga, *Halidrys siliquosa*.

Amathia guernseii sp. nov.
(Fig 2A, 6B, 7B)

Holotype: BMNH; 1898.5.7.189, Saints Bay, Guernsey.

Paratypes: BMNH; 1912.12.21.682, Guernsey. 1967.8.10.2, Scilly Is. 1984.2.26.31, Gulland Rock, Padstow, Cornwall.

ETYMOLOGY. The species was first recognised in material from Guernsey.

DESCRIPTION. In the erect part of the colony, branching is primarily bifurcate, ranging from equally dichotomous, to almost rectilinear series with side branches. The angle between sister stolons remains approximately 60 deg. There is a strong disposition towards the rectilinear condition where at a bifurcation one daughter stolon tends to remain in line with the main axis of the maternal stolon; the other daughter stolon appears sequentially on alternate sides, produced at approximately the same distal inclination to the maternal stolon axis as the maternal stolon autozooids. The lateral angular inclination of this daughter stolon is about 30 deg. to the orientation of the maternal autozooid group. Autozooid groups occur at the extreme distal ends of stolons, frequently overlying the subsequent branching point. Stolons are usually shaped in accommodating the autozooids, being deflected posteriorly at the proximal end of the autozooid group. At their distal ends, stolons often broaden, as if to subdivide, providing bases for the subsequent daughter stolons, and usually curving anteriorly around the distal end of the autozooid group. Occasionally a trifurcation occurs, three daughter stolons being produced. The third stolon arises from a posterior projection at the broadened distal end of the maternal stolon; viewed anteriorly, this region retains a bilateral symmetry. At the proximal end of the autozooid group, autozooids are inclined distally at about 30 deg. to the stolon main axis. The autozooid group profile tends to be level at the proximal end of the autozooid group, decreasing at the distal end; this is due in part to increasing inclination of the autozooids, and in part to diminishing autozooid height. The profile of the rims of the autozooids usually reflects the angle of inclination in having a stepped appearance. Viewed anteriorly, a proximal-most autozooid is usually evident in each autozooid group. The occurrence of this autozooid, the pattern of autozooid displacements, and the succession states of autozooid displacements on the stolons, is identical to that found in *A. lendigera* (see page 313). The orientation of autozooids about the stolonal axis is not rigidly preserved from stolon to stolon, with variations up to 90 deg. being possible. Over an area, the sum total of such variations is to an extent self cancelling, so that autozooids, overall, face in approximately the same direction i.e. in towards a central axis, and thus a relatively sheltered colony-bounded space (see page 341). Rhizoids are produced from the anterior face of stolons, just proximal to the autozooid groups. These arise singly, or as a pair, one on either side of the stolon, at about 30 deg. to the orientation of the autozooids.

Sl. 1.75–2.75	Z/S. 50%
Sd. 0.80	Zn. 8–23 (appearing as 4–11 'pairs')
Zh. 0.38–0.50	
Zw. 0.10	

REMARKS. There is much overlap in the characteristics of *A. lendigera*, *A. intermedis* and *A. guernseii*, and it can be very difficult to distinguish among them unless there is an adequate amount of material. *A. guernseii* may be distinguished on the following basis: the autozooids of *A. guernseii* have a pronounced distal inclination through the entire autozooid group, whereas they tend to remain erect in *A. intermedis*; in *A. lendigera*, the condition of the autozooids is intermediate. *A. guernseii* is the only species of the three to produce rhizoids. This in turn affects the overall form of the colonies; *A. lendigera* and *A. intermedis* being diffuse, (the latter also tending to be less compact), whereas *A. guernseii*, with its aggregating rhizoid system, has a more organised and directional appearance. These differences would appear to be independent of the type of substratum. The description of *A. lendigera* given by Prenant and Bobin (1956) probably includes *A. guernseii*, as they mention the presence of rhizoids. In all three species, some twist of the stolons can occur and this is reflected in the autozooids, but it is never consistent throughout the colony, as in *A. pruvoti* (see pages 336, 337).

As with *A. lendigera*, the displacement of the proximal-most autozooids in maternal and daughter stolons may reflect the timing of the production of the daughter stolons relative to each other (see page 314).

The holotype is an alcohol-preserved specimen, originally a single colony, now divided into two fragments. The substratum is not present in any of the specimens examined.

DISTRIBUTION. The species is known only from the localities of the type material.

Amathia populea Busk MS in d'Hondt, 1983
(Figs 2B, 6D, 7D)

Amathia lendigera: O'Donoghue & de Watteville, 1944: 430.
Part *Amathia populea* Busk MS in d'Hondt, 1983: 97, pl. 3 (4).
Not part *Amathia populea* Busk MS in d'Hondt, 1983: 65, (=*A. woodsii*).

MATERIAL EXAMINED

Lectotype (selected here): BMNH; 1899.7.1.526, Natal, S.A., Busk Collection.

Paralectotypes: BMNH; 1822.8.22.1, Port Alfred, Pondoland, S. Africa. 1851.3.12.36, Port Natal, S. Africa 1899.7.1.112 C, 513, 540, Algoa Bay, S. Africa.

OTHER MATERIAL

BMNH; 1886.7.2.9, 1985.3.4.1, Algoa Bay, S. Africa. 1942.8.6.15, Isipingo Beach, Durban, S. Africa. 1963.2.14.7, Cape of Good Hope.

MM; 7061/2, Grahamstown, S. Africa. 7062/2, S. Africa. 7076/2, no locality. 7077/2, Cape Agulhas, S. Africa.

DESCRIPTION. In the erect part of the colony, branching is bifurcate; rarely, a trifurcation occurs. At a bifurcation, the two daughter stolons are produced laterally to anterolaterally, at approximately 30 deg. and 60 deg. to the maternal stolon axis, respectively. The two angular displacements may vary, but occur on alternate sides at successive bifurcations. Development in parts of the colony may be directionally biased giving rise to plumes of stolons. Plumes may be up to 7 cm. in length, with those stolons forming the central axis appearing sympodially arranged. This axis is in fact a simple linear series of stolons with lateral branches occurring on alternate sides. Side branches within a plume are usually limited to 4 or 5 stolons in sequence. As a result of daughter components frequently being produced in a slightly anterior direction, plumes are arc-shaped to cylindrical in cross-section. All sequences end with the production of paired lanceolate processes, each process made up of 2–3 sequential, progressively tapering kenozooids. Sometimes, the production of a stolon in a side branch is replaced by that of a lanceolate process. Autozooid groups reach to the distal ends of stolons, frequently overlying the subsequent branching point. Stolons are usually shaped in accommodating the autozooids, appearing raised at the proximal end of the autozooid group, becoming shallower distally and usually curving anteriorly to the region of bifurcation. Autozooids are outer-wall thickened, but they often appear cylindrical. Autozooid group profile diminishes distally, in part due to stolon shape, in part due to decreasing autozooid height. Autozooids incline distally at about 30 deg. this being displayed at the autozooid rims, the rims usually having a stepped appearance. Viewed anteriorly, a proximal-most autozooid is usually evident in each autozooid group. The occurrence of this autozooid, the pattern of autozooid displacements, and the succession states of autozooid displacements on the stolons, are identical to those found in *A. lendigera* (see page 313). As one daughter stolon tends to remain in line with its maternal stolon, the alternating sequence of autozooid displacements on linear series of stolons is more prominent. The orientation of autozooid groups is generally well preserved from stolon to stolon. Rhizoids may be produced at the proximal end of stolons, most frequently from those in the central axis regions of plumes. Where rhizoids are produced, it is as one per stolon, each arising usually from the outer faces of bifurcations, orientated at between 90–180 deg. to the autozooids on the same stolon. The resulting colony form is usually arborescent. Secondary development may occur in the erect part of the colony where stolons in the common bases of plumes resume normal budding of daughter stolons. The angular displacements described above are retained, but without maintaining the autozooid orientations about the stolons, or the directional organisation evident elsewhere in the colony. The ensuing compact, cotton-wool like, mass may engulf the plume and trunk regions.

Sl. 1.00–1.40	Z/S. 30–55%
Sd. 0.13–0.18	Zn. 6–13 (appearing as 3–6 ‘pairs’)
Zh. 0.38	Tpl. 1.75 (2.60 max.)
Zw. 0.10–0.13	

REMARKS. An association with a sandy environment is inferred from the sand grains sometimes found accreted to rhizoids and attached epizoic worm tubes. In plume portions of the colony, the preserved orientation of the autozooid groups, and the cross-sectional profile of the regions, results in autozooids facing into a relatively sheltered colony-bounded space (see page 341).

The plume portions of *A. populea* strongly resemble the figures of *A. lemanii* in the unpublished plates of Lesueur. However, it is equally possible to draw a similarity between these figures and *A. woodsii* (see page 324) or possibly portions of *A. tricornis*.

Understandably, *A. populea* has, in the past, been confused with *A. woodsii* and *A. tricornis* (e.g. d’Hondt, 1979, 1983). It has also been confused with *A. lendigera* (e.g. O’Donoghue and de Watteville, 1944, BMNH 1942.8.6.15). *A. populea* may be distinguished from *A. lendigera* (and similar forms *A. guernseii* and *A. intermedis*) primarily through the occurrence and location of rhizoids. These do not occur in *A. lendigera* or *A. intermedis*. In *A. guernseii*, the rhizoids are produced anteriorly, just proximal to the autozooid group; whereas in *A. populea* they are produced latero-posteriorly and proximally distant from the autozooid group. *A. tricornis* and *A. populea* differ in many characteristics (see page 321).

D’Hondt (1979) placed *A. populea* Busk MS (part, without qualification) into synonymy with *A. cornuta* (*sensu* d’Hondt, 1979) along with a number of other species, including *A. australis*. D’Hondt (1983) then drew some distinction, first indicating (p.65) that *A. populea* Busk MS part from Australia is synonymous with *A. cornuta* (*sensu* d’Hondt, 1983 i.e. *A. woodsii* see pages 320, 323 *et seq.*). Later, d’Hondt (1983: p.97) also gave a brief description and a figure (p.103) of a South African specimen, BMNH 1899.7.1.526 of *A. populea* Busk MS part, so validating Busk’s manuscript name, and making the name *A. populea* available for this species. D’Hondt referred to the specimen as ‘A.sp.’ yet appears to have remained equivocal by suggesting that this is also possibly ‘a form of *A. cornuta*?’ (*sensu* d’Hondt, 1983) i.e. *A. woodsii* (see pages 320, 323 *et seq.*).

A. populea and *A. woodsii* may be distinguished in the following: the form of the lanceolate processes, being simple in *A. populea*, often branched in *A. woodsii*; the autozooid to stolon ratio, being higher in *A. woodsii*; the orientation of the rhizoid origins, being latero-posterior in *A. populea* and anterior in *A. woodsii*.

Small quantities of material may be very difficult to distinguish and identify with certainty, such that even Busk made errors. Some of Busk's *A. populea*, BMNH 1899.7.1.528 from Algoa Bay, South Africa and BMNH 1899.7.1.4383 from Australia, is in fact *A. woodsii*. BMNH 1899.7.1.4383 is the only specimen in the BMNH collections from Australia labelled *A. populea*, and so is undoubtedly the material that d'Hondt (1983) refers to under the name '*A. populea* Busk, unpublished (pars: Australia)'.

All specimens labelled by Busk as *A. populea* and considered by d'Hondt (1983) are certain syntype material. D'Hondt's figured specimen, (BMNH 1899.7.1.526) is here chosen as lectotype, the remaining Busk material, except for the two misidentifications indicated above, has paralectotype status.

DISTRIBUTION. The species is known from the south-eastern coast of South Africa, possibly also occurring off southern Australia.

Amathia woodsii Goldstein, 1879
(Figs 2C, 9B, D)

Amathia woodsii Goldstein, 1879: 20, pl. 3 (fig. 5).
Amathia australis: MacGillivray, 1889: 310, pl. 185 (figs 5, 5a).
Amathia woodsii: MacGillivray, 1895: 138, pl. B (figs 5, 5a).
Part *Amathia cornuta*: d'Hondt, 1983: 65, fig. 36 (C).

MATERIAL EXAMINED

Neotype (selected here): BMNH; 1883.11.29.27, Port Jackson.

OTHER MATERIAL

BMNH; 1861.9.20.17, Fremantle. 1897.5.1.1189, no locality. 1897.5.1.1196, Port Phillip Heads. 1899.7.1.528, 1985.3.6.1, Algoa Bay, S. Africa. 1899.7.1.4383, Australia. 1909.8.4.10, Western Port, Australia. 1963.3.28.4, Adelaide.

MM; 7075/2, Queensland.

DESCRIPTION. In the erect part of the colony, branching is bifurcate. Stolons are arranged to form rectilinear series with side branch stolons. Side branch stolons are produced on alternate sides at each subsequent bifurcation, arising with the same distal inclination as the autozooids of their maternal stolons. The lateral angular displacement of the side branch stolons can be 0–90 deg. to the autozooid orientation, but usually ranges from 10–30 deg. In parts, growth appears favoured along the rectilinear series, with side branches usually restricted to 4–5 stolon units either side. These parts of the colony have a plume like appearance. Branches end with a pair of lanceolate terminal processes, usually produced in the same orientations as stolons. The processes are made up of 3–4 sequential, progressively tapering kenozooids, often bifurcating at the distal end of the basal segment kenozooid. The lanceolate processes in which bifurcation occurs are most usually produced in the non-rectilinear position. Frequently, the production of a side branch is replaced by the production of a lanceolate process, emphasising the appearance of directional growth. Autozooid groups occur towards the distal ends of stolons, but often there is further autozooid-free part, coinciding with the production of a side branch component. Stolons may show a gentle anterior curvature, and sometimes curve around the distal autozooids of a group. Autozooid group profile diminishes distally, mainly due to decreasing autozooid height, but sometimes due in part to an increase in their distal inclination. Autozooids are outer-wall thickened, the walls appearing cylindrical. Viewed anteriorly, a proximal-most autozooid is usually evident in each autozooid group. The occurrence of this autozooid, the pattern of autozooid displacements, and the succession states of autozooid displacements on the stolons, are identical to those found in *A. populea* (see page 318). The orientation of autozooid groups is generally well preserved from stolon to stolon. Along a plume therefore, autozooids on the rectilinear sequence all face in the same direction, with lateral stolon autozooids generally facing across these. Rhizoids may be produced, one per stolon, arising near to and at about the same orientation as the autozooids. Colony arrangement is similar to *A. populea*.

Zh. 0.65
Zw. 0.10
Sl. 2.58
Sd. 0.20

Z/S. 50–70%
Zn. 8–23 (appearing as 4–11 'pairs')
Tpl. 2.50 (4.80 max.)

REMARKS. Goldstein's account and figure are a very good representation of the species; the only omission is information on rhizoid production. D'Hondt (1983) placed the species in synonymy with *A. cornuta* Lamarck (1816), but there is some doubt as to the identity proposed for Lamarck's specimen by d'Hondt (1983), and the distinction between *A. cornuta* Lamarck and *A. woodsii* is here maintained (see page 323 *et seq.*).

With limited material, confusion could arise between *A. woodsii* and *A. populea* or *A. tricornis*. D'Hondt (1983) has referred specimens of these last two species to *A. cornuta* Lamarck (*sensu* d'Hondt 1983), i.e. *A. woodsii*. The species may be distinguished in the following: the presence of the characteristic subdivided lanceolate process in *A. woodsii*, this being simple in the other two; the production of rhizoids being near to, and in the same orientation as the autozooid group in *A. woodsii*, these being distant, and of different orientation in the other two; the budding pattern in *A. woodsii* is never as complex as in *A. tricornis*, and the predisposition to rectilinear development is more prominent than in *A. populea*, in which there is a tendency for a sympodial appearance.

According to Stach (1936) specimens from Goldstein's collection were deposited in the NMV. However, his material for *A. woodsii* is not there (NMV in litt. 6.12.1984). In view of the confusion which has arisen, there is a need for type material. The description and measurements given here are based on BMNH 1883.11.29.27 from Port Jackson, an alcohol specimen, rehydrated from the dry state. The specimen is here selected as neotype. Goldstein does not give a locality for his specimen, only mentioning that the species was found on a previous occasion at Portland, presumably Victoria State.

DISTRIBUTION. The species is known from the south-eastern coast of South Africa, and from Australia, with records from Fremantle, Adelaide, Port Phillip Heads, Port Jackson and 'Queensland'.

Amathia tricornis Busk MS

(Figs 2D, 12C)

Holotype: BMNH; 1899.7.1.6600, Australia, Busk Collection.
Paratypes: BMNH 1899.7.1.4393, 4394, Australia, Busk Collection.

ETYMOLOGY. Busk's MS name, probably indicating the occurrence of three terminal lanceolate processes.

DESCRIPTION. In the erect part of the colony, branching is mainly trifurcate, although tetrafurcation occurs in certain regions. The latter condition is associated with astogenetically early parts of the colony, which form the base and central main-axis regions. These regions tend to be composed of lengthy series of, what are here termed, type 'a' stolons. Type 'a' stolons are longer than other type 'b' stolons found in the trifurcate portions of the colony, and often bear rhizoids. Where rhizoids are produced, these arise from the proximal end of a stolon, usually singly, at between 45–90 deg. to the autozooid orientation on the same stolon. Autozooids borne by type 'a' stolons show no difference in size from those on type 'b' stolons, although the autozooid groups tend to be shorter. The linear proportion of stolon occupied by autozooids, therefore, is lower. The stolon budding arrangement, in both tri- and tetrafurcate conditions, always results in one daughter stolon lying in rectilinear succession to the maternal stolon. Two other daughter stolons are produced laterally, one on each side, at about 60 deg. to this central axis. All three of these daughter stolons bear autozooids, usually orientated in the same direction as those on the maternal stolon, with some exceptions. In the tetrafurcate condition, a fourth daughter stolon is produced, also at about 60 deg. to the central axis, but posteriorly to the maternal stolon. The autozooid group orientation of the maternal stolon is preserved in this daughter component; the autozooid group thus faces distally along the rectilinear series of the central axis (see Fig. 2D). In the tetrafurcate condition alone, the orientation of the autozooid groups along the rectilinear series is not always maintained. A repeat rotation of 90 deg. may, instead, be observed at each axial junction. The relationship of sister daughter stolons to the axial daughter stolon remains fixed, and, thus, the entire assemblage follows the re-orientation. The original orientations are recovered every fourth axial stolon unit along the sequence. In the trifurcate condition, lateral growth appears to be limited to one or two stolons in sequence each side. Development in these parts of the colony is therefore directionally biased and these parts have a plume like appearance. Branches end with the production of three lanceolate terminal processes, each made up of two or three sequential, progressively tapering kenozooids. These arise from, and lie approximately in line with, their maternal stolons. Sometimes, the central terminal process does not form, being replaced by a stolon instead. This may be repeated so that occasionally, lateral branches may be several stolons in length. On both type 'a' and type 'b' stolons, autozooid groups occur at the extreme distal end of stolons, frequently overlying the subsequent branching point. Autozooid group profile diminishes distally in all cases, mainly due to increasing distal inclination of the autozooids. In all parts of the colony, autozooids are outer-wall thickened. Along rectilinear sequences of stolons, there is a predictable repetition in the arrangement of the autozooids borne. The sequence, progressing distally, is as follows: if, in an autozooid group, there is one proximal-most autozooid prominent, this is associated with one side of the stolon; in the next stolon, no single autozooid is prominent proximally, the proximal autozooids being paired equally; on the third stolon, a proximal-most autozooid is prominent once again, but on the opposite side to that of the first stolon; on the fourth stolon, the proximal autozooids are paired as on the second stolon; the fifth stolon repeats the arrangement on the first stolon. On laterally branched stolons, a proximal-most autozooid is prominent, and is associated with the side nearest the rectilinear stolon sequence. Autozooids on stolons continuing in rectilinear series which develop from lateral branch stolons subsequently follow the predictable pattern of repetition given above.

Sl.	(a) 2.10	Z/S.	(a) 30–40%
Sd.	(a) 0.25	Zn.	(a) 8–11 (appearing as 4–5 'pairs')
Sl.	(b) 1.45	Z/S.	(b) 60%
Sd.	(b) 0.25	Zn.	(b) 10–21 (appearing as 5–9 'pairs')
Zh.	0.35		(all autozooids)
Zw.	0.10		(all autozooids)
Tpl.	2.10		

Remarks. No evidence exists, in the limited material available, that the trifurcate condition ever gives rise to the tetrafurcate condition. The colony form is inferred to be arborescent, resulting from the production of rhizoids.

None of the material held at the BMNH named *A. tricornis* in MS by Busk is misidentified. D'Hondt (1979 & 1983) erroneously placed this species in synonymy in part, with parts of *A. cornuta* (Lamarck) *sensu* d'Hondt (i.e. *A. woodsii,* see page 323), and in part, initially with *A. pinnata* (1979) (see page 330), and subsequently with *A. inarmata* (1983) (i.e. *A. biseriata,* see page 332). D'Hondt on each occasion mentioned *A. tricornis* in synonymy only, thus not making the name available at any time (I.C.Z.N. article 11e).

Among the species which may be confused with *A. tricornis* are: *A. populea*; *A. woodsii*; *A. pinnata*; *A. biseriata*. In brief, *A. tricornis* has a more complex colony construction and differs from these species in many features, for example: the bimorphic autozooid-bearing stolons; the normal occurrence of tetra- and trifurcation, including the production of triplet lanceolate processes and their permutations with autozooid-bearing stolons; autozooid and stolon re-orientations; the productions site of the rhizoids. There are also differences in the autozooid to stolon ratios.

Distribution. The species is known only from material described as being from 'Australia', sent to Busk by Miss Gore.

Amathia lamourouxi nom. nov. for
Amathia cornuta auctorem
(Figs 3A, 8C, 9A, C)

? Not *Serialaria cornuta* Lamarck, 1816: 131.
Amathia cornuta Lamouroux, 1816: 159, pl. 4 (fig. 1a, 1B).
? Not *Serialaria australis* Tenison Woods, 1877: 83, 1st fig.
? Not *Amathia australis*: Tenison Woods, 1880: 102.
Amathia cornuta: Tenison Woods, 1880: 99, fig. 3.
Not *Amathia australis*: MacGillivray, 1889: 310, pl. 185 (figs 5, 5a), (= *A. woodsii*).
Amathia cornuta: MacGillivray, 1895: 137, pl. D (fig. 1, 1a).
? *Amathia cornuta*: d'Hondt, 1979: 10, 16.
Part *Amathia australis*: d'Hondt, 1983: 65, fig. 36(F).
Not *Amathia cornuta*: d'Hondt, 1983: 65, fig. 36(C) (= *A. woodsii*).

MATERIAL EXAMINED

Neotype (selected here): BMNH; 1887.12.10.70, Port Phillip, J. B. Wilson collection.

OTHER MATERIAL

BMNH; 1842.11.4.50, Sydney. 1899.7.1.3, New Zealand. 1899.7.1.4325, Victoria. 1899.7.1.4327, 4329–31, 4333, Australia. 1899.7.1.4328, Bass Strait. 1899.7.1.4334, Australia & New Zealand. 1985.3.10.1, Flinders Is., Bass Strait. 1985.3.24.1, mid channel, Port Phillip Heads, 15 m.

MM; 7078/2, Australia.

LBIMM; bry 2821 part, Australie Occidentale/Nouvelle Hollande (see below).

ETYMOLOGY. Lamouroux's name is used for his species of *A. cornuta* (1816), a name preoccupied by *A. cornuta* (Lamarck, 1816).

DESCRIPTION. In the erect part of the colony, branching is bifurcate. At any branching point, daughter stolons may be produced in positions ranging from almost rectilinear, to 90 deg. to the maternal stolon. A minimum separation of 90 deg. occurs between daughter stolons. These usually arise from the posterior side of their maternal stolon. Stolons are narrowed proximally and usually curved anteriorly, being reminiscent of a short, simple, cow horn. Autozooid groups occupy the greater part of stolons, and frequently overlie the subsequent branching point. Autozooid group profile usually increases proximodistally within each group, or may remain level. Autozooids are outer-wall thickened. Viewed anteriorly, a single proximal-most autozooid is evident in each autozooid group. This autozooid is usually placed just off the stolon mid-line, thus associated with either one or other side of the autozoid group. No pattern is evident from group to group, in the location of this autozooid. At the distal end of each autozooid group and contiguous with the autozooids, are produced a pair of tapering, single-kenozooid lanceolate processes. At the distal extremities of the colony, both daughter stolons tend to be produced at 90 deg. to their maternal stolons, i.e. separated from each other in equal dichotomy by 180 deg. In less distal parts of the colony, daughter stolons may be separated from each other in equal dichotomy by lesser angles. Daughter stolons produced in the linear position are less common and are associated with more central and proximal (astogenetically earlier) regions of the colony. Autozooid orientation is generally not preserved from stolon to stolon. Often there is an equal rotation by up to 90 deg. of each daughter stolon in opposite directions i.e. were both daughter stolons to lie in the linear position, their anterior faces would be away from each other. Successive daughter stolons actually lying in the linear position and forming a sequence, are all produced from the same side, i.e. in such a sequence, viewed anteriorly each time, they would all have been budded from e.g. the left side. The orientation of the autozooid groups, in such a linear sequence, is rotated by 90 deg. in the same direction, with each successive stolon. The original orientation is recovered every fourth stolon unit. Superficially, branching can appear as 'alternate' along a linear sequence. Rhizoids may be produced, usually from stolons along these linear sequences. Rhizoids are produced one per stolon, arising from a position level with, and at 90 deg. to the proximal-most autozoid, and on the same side of the stolon as the direction in which the stolon was budded.

Zh. 0.40–0.50
Zw. 0.13
Sl. 1.13
Sw. 0.25 (at the widest region)
Z/S. 75%
Zn. 11–15 (appearing as 5–7 'pairs')
Tpl. 2.00–2.25

REMARKS. No pattern has been discerned in the autozooid arrangement from stolon to stolon, other than, if the proximal-most autozooid of a group is associated with one side of the stolon, then that association may remain in both daughter stolons over a number of successive bifurcations.

The identity of *A. cornuta* auct. is inextricably associated with the collections made by Peron and Leseur, between the years 1800–1804 (see page 307), on which both Lamarck and Lamouroux worked, both of them describing a 'cornuta'.

Tenison Woods (1880) drew a distinction between his *A. australis* and *A. cornuta sensu* Lamouroux (i.e. *A. lamourouxi*) based on the understanding that Lamouroux's (1816) figure indicates a single line of autozooids. Lamouroux himself, referred in the singular to 'the largest cell of each group . . . garnished with two setaceous appendages'. The misinterpretation of a single row for a double row of autozooids, might be made as a result of a preservation artifact where, in dried specimens, the thinner central walls between autozooids collapse from view, leaving only the outer walls visible. On this basis there is no distinction between *A. australis* and *A. lamourouxi*. The additional difference claimed by Tenison Woods, in the form of the 'setaceous appendages' (his figure of 1877 shows these as being broad and less trim than those in Lamouroux's figure), might be accounted for in terms of the variation which may occur within *A. lamourouxi*. However, Tenison Woods' figure (1877) shows clearly that his specimen had undergone trifurcation. Two possibilities may account for this: the first, that under certain conditions, *A. lamourouxi* can undergo such a division; the second, that Tenison Woods did in fact have a separate species. Although the former may be possible, trifurcation has not been recognised in specimens here assigned to *A. lamourouxi*. The whereabouts of Tenison Woods' material is not known.

MacGillivray (1889) considered *A. australis* to be *A. cornuta sensu* Lamouroux, but in his description (p.310) and figure (pl. 185, figs 5, 5a) gave an acocunt of *A. woodsii*. MacGillivray (1895) subsequently recognised the error, and correctly referred to his account of 1889 as being descriptive of *A. woodsii*. At the same time, MacGillivray distinguished between *A. woodsii* and *A. cornuta*, and reaffirmed his opinion that *A. australis* was synonymous with the latter, but gave Lamouroux as the author and placing Lamarck in synonymy.

D'Hondt (1979) has found a specimen, LBIMM bry 2821, which is claimed to be the holotype of *A. cornuta* (Lamarck). D'Hondt (1979) placed *A. australis* in synonymy under *A. cornuta* (Lamarck), but without mention of *A. woodsii*. D'Hondt (1983) then placed *A. woodsii* in synonymy under *A. cornuta* (Lamarck), but excluded *A. australis*, thus revoking his opinion of 1979 and indicating that *A. australis* is different (d'Hondt's reference to 'parts' of *A. australis* at this point are enigmatic). In this reorganisation of the species, d'Hondt (1983) gave two figures: 36(C) as *A. cornuta* (Lamarck), and 36(F) as *A. australis*. Figure 36(C) is in fact *A. woodsii*, and 36(F) is *A. cornuta*, both of common usage, the latter corresponding with Lamouroux (1816), of which *A. australis* is usually taken to be a junior synonym.

D'Hondt (1983) appears to have determined *A. cornuta* (Lamarck) to be different from *A. cornuta* Lamouroux. *A. cornuta* (Lamarck) predates *A.* cornuta Lamouroux (Tenison Woods, 1880, d'Hondt, 1983). D'Hondt (1983) thus relegated *A. woodsii* as a junior synonym of *A. cornuta* (Lamarck), and assigned the name *A. australis*, as the next available name, for what was previously accepted as *A. cornuta sensu* Lamouroux.

Unless it was the only specimen involved, LBIMM bry 2821 can only be taken as the holotype if so designated at the time of introduction by the original author. Lamarck (1816) did not do this, and the number of specimens involved is not certain.

LBIMM bry 2821 is recorded as being one of three specimens of *A. cornuta* so identified by Lamarck and in the Paris Museum at the time of the compilation of the first catalogue of Bryozoa in 1867. The other two specimens appear to have been *A. cornuta sensu* Lamouroux, only 'possibly' originating from Peron and Lesueur. Their locality is given as 'Australasie'. The specimens were numbered: 172a,b,c. (photocopy of the 1867 catalogue). LBIMM bry 2821 is the only one of the three which is known to have come from Peron and Lesueur (d'Hondt in litt. 10.12.1984). The locality for this specimen is 'Australie Occidentale' (d'Hondt, 1979), and also as 'Nouvelle-Holland' (loan form 24th Jan. 1985).

D'Hondt (1979) reported that LBIMM bry 2821 carries the label 'Amathia lemanii Lesueur'. This would appear to be in the hand of Pergens, the original label having been lost or destroyed. The specimen is taken to be the same one that Pergens (1887) correlated with a figure in the unpublished plates of Lesueur, these in turn related to a manuscript of Desmarest and Lesueur, deposited at Paris in 1829 (with another slightly different version at le Havre). Pergens (1887, p. 88) ascertained that plate 13, figure 6, in the unpublished plates, is *Amathia lemanii*, and (p. 90) then gave the identification he was able to make of the species in terms of what was, to him, a valid and available name i.e. *A. cornuta* (Lamarck). Copies of the plates of Lesueur exist at the BMNH. Plate 13, figure 6, consists of three representations of the species intended, all three at different magnifications. The species represented could be *A. woodsii* or *A. populea* (see page 318); both species are capable of assuming the characteristics portrayed. Missing from the figure(s) is any information on rhizoids and on any occurrence of the characteristic subdivided terminal filaments, which might serve to distinguish between the two species. Only the actual specimen used by Lesueur will determine the true species (taken to be LBIMM bry 2821). The identity of this species is of little taxonomic consequence however, as neither plates nor descriptions have ever been published. LBIMM bry 2821 could have been the holotype perhaps, of Desmarest and Lesueur's species, but there is insufficient evidence published to suggest that it was that of Larmarck's.

In addition, Larmarck (1816) gave no figure, specimen number, or dimensions, with which a specimen may be correlated. Furthermore, the locality information (see above) for the specimen, although close, does not match exactly with that of Lamarck (or of Lamouroux). Lamarck gives 'l'Ocean asiatique' (Lamouroux gives 'Sur les Fucus de l'Australasie'). That the specimen was part of Peron and Lesueur's collections, may not in this case be sufficient; Lamarck himself is not definite as to the origins of his specimen, only 'believing' it to be from Peron and Lesueur. Pergens (1887) merely expressed his opinion that LBIMM bry 2821 is the same as *A. cornuta* (Lamarck); how he reached that conclusion is not clear. The specimen appears to be only one remaining of a number, others having gone astray since the days of Peron and Lesueur; the 1867 catalogue of the Bryozoa was compiled some 51 years after Lamarck's publication.

It is possible that LBIMM bry 2821 may be eligible for selection as lectotype of *A. cornuta* (Lamarck), if it can be shown to have been part of Lamarck's original syntype series, and formative of his opinion. However, Larmarck did also identify two different specimens as being his species, these being *A. cornuta sensu* Lamouroux (see above). These specimens might also have been eligible for selection, but are no longer to be found in the Paris Museum (d'Hondt in litt. 10.12.1984, 24.01.1985).

Further challenge to the identity proposed by d'Hondt for *A. cornuta* lies in the evidence that preceeds Pergen's opinion (1887). Tenison Woods (1880) gave information on the working relationship between Lamarck and Lamouroux concerning the *Amathia* specimens collected by Peron and Lesueur. Much of the information appears to be derived from Lamouroux's (1816) own preface and introduction. Lamouroux had 'the fullest access' to Lamarck's collection, and named at least part of this, if not all of it.

Neither Lamarck's (1816) nor Lamouroux's (1816) account of a 'cornuta' contradicts the other. However, whereas Lamouroux's account is quite explicit, and furnished with figures, such that the species he described may still be recognised; Lamarck's account is open to interpretation. The descriptions may be translated as follows:

Lamouroux, p. 159: No. 266.
(from the French)—The largest cell of each group having its free border, garnished with two setaceous appendages.
(from the Latin)—two setaceous filaments from the first rank cell
Lamarck, p. 131: No. 2.
(from the French)—I believe it (to be) from the voyage of Messieurs le Sueur and Peron. It is a

little more stout and less capillary than the preceeding [i.e. *A. lendigera*], at the extremities curved and as curls.
(from the Latin)—very branched, articulated, somewhat curled; branches alternate; curved secondary little branches; cells in distinct series; two setae at the most distant extremity.

In Lamarck's account, no orientation is given for the setae, and the description could apply to *A. cornuta* of Lamouroux, *A. woodsii* or *A. populea*. Whether the reference to the secondary branches is an indication of an arborescent growth form i.e. axial development with lateral branch system, or a reference to the stolons themselves, is not clear. In either case, the description is insufficiently distinctive. Branching is alternate in *A. woodsii* and *A. populea* and may appear so in *A. cornuta sensu* Lamouroux. Finally, Lamarck makes no mention of any subdivided terminal processes (present in LBIMM bry 2821 part) to be expected if his 'cornuta' was the equivalent of *A. woodsii*.

Although it is not possible to recognise a single species from Lamarck's description, the identity of *A. cornuta* (Lamarck) has been understood through the later accounts of the two authors: in Lamouroux (1824) and Lamarck (1836) respectively, each recognises the other's *A. cornuta* as synonymous with his own; from this derives the *A. cornuta* of common usage. It is this concordance which d'Hondt (1983) has in effect repudiated.

In the strictest sense, *A. cornuta* (Lamarck) should have been classed as a *nomen dubium*, and not used. This is historically implied by Tenison Woods (1880) who acknowledged that Lamarck probably predated Lamouroux, and so accepted *A. cornuta* (Lamarck), 'but with reference to Lamouroux only'. MacGillivray (1895) appears to have been of the same opinion (see above).

In the light of such contradictions, Lamarck's *A. cornuta* must be taken as a *nomen dubium*, and the name should no longer be used for Lamouroux's species. *A. australis* of Tenison Woods would be the next valid name available, if certainty could be attached to the identity of his species (see above). Under these circumstances, it is wiser, in the interest of long term stability, to select a new name for *A. cornuta* Lamouroux, accepting either his figures as lectotype, or perhaps selecting a neotype. It is here proposed that *A. cornuta* auct. be known as *A. lamourouxi*, with specimen BMNH 1887.12.10.70 as neotype.

DISTRIBUTION. The species is recorded from New Zealand and southern Australia.

Amathia plumosa MacGillivray, 1890
(Figs 3C, 12A, B)

Amathia plumosa MacGillivray, 1890: 110.
Amathia plumosa: MacGillivray, 1895: 139, pl. C (figs 2, 2a).
Amathia plumosa: d'Hondt, 1983: 67, fig. 36 (B).

MATERIAL EXAMINED
Holotype: NMV; H494, Port Phillip Heads, J. B. Wilson Collection.

OTHER MATERIAL
BMNH; 1963.2.12.354, 358, Western Australia. 1985.3.8.1, no locality.

DESCRIPTION. The branching pattern on the erect part of the colony is based on both bi- and trifurcation. Trifurcation is associated with non autozooid-bearing stolonal kenozooids, forming angularly undulating 'main-stems'. At the distal end of each of the main-stem constituent stolonal kenozooids, are produced: a single continuing stolonal kenozooid, deflected by approximately 30 deg. towards the central axis of the main-stem; two (autozooid-bearing) side branch stolons, one each side. The side branch stolons are produced in the same plane as their maternal stolonal kenozooid, but diverge from each other equally, by an approximate total angle of 60 deg. The autozooids borne on these side branch stolons face the main-stem, and the stolons themselves are curved anteriorly. Subsequent branching from these side branch stolons is usually bifurcate, although new main-stem sequences may be produced, showing the associated trifurcation. Development along side branches is usually limited; 2–3 stolons in a sequence is usual, but up to 8 stolons in succession may occur. The orientation of autozooid groups along any such sequence remains the same. These side branches end with the production of a pair of usually dichotomously branched lanceolate processes. These are made up of sequential, progressively tapering kenozooids. Where the processes are branched, this occurs at the distal end of the base segment kenozooid. This may be repeated in one or both of the next resultant segments. Rarely, a lanceolate process may trifurcate. On occasions, the production of a stolon in a side branch is replaced by the production of a lanceolate process. Development in such cases, therefore, tends to be directionally biased. The colony is composed of such quasi-cylindrical assemblages, circular in cross-sectional profile, and somewhat reminiscent of 'feather boas'. These may be supported on a trunk-like part of the colony, resulting from the production of rhizoids (see page 309). Rhizoids are produced in two ways: they may be produced from the proximal end of main-stem kenozooids, sometimes singly, although more often as an adjacent pair, in the same orientation as the side branch stolons lying immediately proximal; they may be produced from autozooid-bearing stolons, at approximately 120 deg. to the orientation of the autozooid group on the same stolons. Where autozooid groups develop in side branches, these occur towards the distal ends of stolons, but often there is a further autozooid-free portion. This portion is about the same length as the diameter of, and coincident with the production of, a daughter component. Autozooid group profile tends to remain level and autozooids are outer-wall thickened. Where a proximal-most autozooid of a group is evident, its occurrence, and the pattern of autozooid displacements from stolon to stolon, are similar to those of *A. lendigera* (see page 313) except that the second succession state does not appear to occur.

kSl. 1·45 (main-stem kenozooidal stolons)
kSd. 0·19–0·29 (main-stem kenozooidal stolons)

Sl. 1·03–1·61 Z/S. 55–65%
Sd. 0·15–0·26 Zn. 7–17 (appearing as 3–8 'pairs')
Zh. 0·32
Zw. 0·10

REMARKS. The species is so distinctive that it does not appear to have been confused with any other. The slide mounted specimen NMV H494, is accepted here as the holotype of *A. plumosa* MacGillivray (1890), and as that figured by MacGillivray (1895). The label on the slide carries the information: 'H494 *Amathia plumosa* McG P.P.H. fig J.B.W.'. This in agreement with the original description in which the locality is given as 'Port Phillip Heads', from the collection of J. B. Wilson. The description given here is based on the above specimen. Some supplementary information is derived from BMNH 1963.2.12.354 and BMNH 1963.2.12.358, these agreeing well with the holotype.

There is some indication that the repeated branching in the lanceolate processes coincides with the development of a lanceolate process in substitution for an expected stolon, although there is no certainty to this. Autozooid groups are orientated about main-axis stolons to face into relatively sheltered, colony-bounded space (see page 341).

DISTRIBUTION. The species is known only from Australia, recorded from 'western' Australia and the type locality of Port Phillip Heads in the south-east.

Amathia obliqua MacGillivray, 1985
(Figs 3D, 8B)

Amathia obliqua MacGillivray, 1895: 135, pl. B (figs 2, 2a).

MATERIAL EXAMINED

Syntypes: NMV; H493 (old number 65391), H493 (old number 65392), Port Phillip heads, J. B. Wilson Collection.

OTHER MATERIAL

MM; 7108/2W, Port Phillip.

DESCRIPTION. In the erect part of the colony, branching is bifurcate with repetitive gradual variation evident in the branching angle. This ranges from equal dichotomy, to the condition where the daughter stolons are produced at angles to the maternal stolon axis of 30 deg. and 60 deg. respectively. This variation occurs over a sequence of four stolon units, i.e. if one daughter stolon is angled at 60 deg. to the right of a maternal stolon, the same angular displacement appears, to the left of a maternal stolon, four stolon units further on in a stolon sequence. The original angular displacements are recovered after a further sequence of four stolon units. In between each of these stages, there is an intermediate, equally dichotomous condition. Over the entire sequence, a sigmoidal pattern in stolon arrangement may be observed. Autozooid groups occur towards the distal ends of stolons, but usually there is a further autozooid-free portion beyond the group, of variable length. Stolons tend to be straight, but sometimes the distal autozooid-free portion may be twisted slightly or deflected anteriorly, or both. Autozooid groups are set obliquely on the stolons. The autozooid group points in the same direction as that, in which the bearing stolon itself was budded i.e. viewed anteriorly, on a right hand daughter stolon, the autozooid group starts proximally on the left of the stolon and finishes distally on the right, and vice versa. Autozooid group orientation is generally well preserved from stolon to stolon, though variations of up to 30 deg. may occur. Autozooids are outer-wall thickened, and the autozooids of any one group tend to be about the same height. Autozooid group profile therefore tends to be level. A single proximal-most autozooid is usually prominent in each autozooid group. Its occurrence, and the pattern of autozooid displacements from stolon to stolon, are similar to those of *A. lendigera* (see page 313) except that the second succession state does not appear to occur. Rhizoids may be produced, one per stolon, from mid-way along the proximal autozooid-free end. These are orientated at about 90 deg. to the autozooids, on the outer faces of stolons at a bifurcation i.e. on the side of a stolon away from its sister stolon.

Zh. 0·39	Z/S. 65%	
Zw. 0·11	Zn. 11–21	(appearing as 5–10 'pairs').
Sl. 1·16–2·13		
Sd. 0·13–0·20 (immediately proximal to the autozooids)		

Remarks. Little material is available for study, therefore little is known of the colony form, other than from MacGillivray's original description. It is inferred, from the presence of rhizoids, that the colony attains an arborescent form. MacGillivray's (1895) description seems to bear this out, the colony being 'attached by the bases of main stems by radical tubes, the branches being quite free and not intertwining or climbing over other objects'. MacGillivray made no mention of the non-erect part of the colony. Neither of the two slide specimens from the NMV, H493 (65391, 65392) matches the figure of MacGillivray (1895) exactly. There is however a very close resemblance to specimen H493 (65391). Some of this colony fragment has broken away which may account for the lack of congruence with the figure.

As with many other species of *Amathia, A. obliqua* has been confused with *A. lendigera* (by MacGillivray 1895). The presence of rhizoids and their orientation, the development pattern of autozooid groups and the overall colony form, serve to distinguish this species from *A. lendigera* (and also from *A. intermedis* and *A. guernseii*).

Distribution. The species is recorded only from the Port Phillip Bay region in Australia.

Amathia wilsoni Kirkpatrick 1888

(Figs 4D, 10C, D)

Amathia wilsoni Kirkpatrick, 1888: 18, pl. 2 (figs 4, 4a).
Amathia wilsoni: MacGillivray, 1895: 139, pl. D (figs 2, 2a, 2b).
Amathia wilsoni: d'Hondt, 1983: 67, fig. 36 (A).

MATERIAL EXAMINED

Syntype: BMNH; 1888.5.17.7, Port Phillip, J. B. Wilson Collection.

OTHER MATERIAL

BMNH; 1821.5.24.16, 1985.3.12.2, Portland, Australia. 1882.7.7.54, Wilsons Promontory. 1886.6.8.3, Port Phillip 1910.10.17.31–32 part, north end Victoria Tasman Cable, <50 fthms. (91.44 m). 1963.2.12.361, Australia 1963.2.12.366, Holdfast Bay nr. Adelaide. 1985.3.12.1a,b, Flinders Is. 1985.3.18.3, Hobart, Tasmania.

MM; 7136/3W, off Shark Is., Port Jackson. 7137/3W, Port Phillip.

Description. In the erect part of the colony, branching is based on tri-, tetra- and pentafurcation. The colony is constructed of three types of stolons, here termed 'a', 'b' and 'c' (see below). Often, the region of branching, of a maternal stolon, is prominently thickened. Pentafurcation appears to be associated with external influence such as injury or the presence of an epibiont. Tetrafurcation is associated with astogenetically early regions, forming the base and main-axis regions of the colony. Main-axis regions are composed of type 'a' stolons. Trifurcation is associated with side branches which develop from main-axis regions. It is not possible to predict with certainty, the direction in which stolons will be produced at pentafurcation. In both the tetra- and trifurcate conditions however, one resultant component is produced in linear succession, and two others are produced laterally, one on each side. These are lateral side branches, composed of type 'b' stolons and are produced at an angle of about 60 deg. to the central axis. In the tetrafurcate condition, the fourth component, comprising type 'c' stolons, is produced posteriorly to its maternal stolon in the central axis, also at an angle of about 60 deg. This is a posterior side branch. Development along the side branches is limited and ends with the production of pinnately arranged, tapering kenozooids. The component kenozooids of such pinnate groupings are arranged as: three in linear succession, with an opposed lateral pair at both inter-kenozooidal junctions. In the lateral side branches, the pinnate kenozooids are usually produced after a 'linear' succession of three stolons; in the posterior side branch, after only one. The orientation of autozooids about the stolon along a main-axis sequence remains the same; this same orientation is preserved in the posterior side branch. In the lateral side branches, the autozooid group orientation is also preserved from stolon to stolon, but the autozooids are usually re-orientated to face distally along the main-axis; also in these branches, only one stolon, of a possible three, is usually produced at each branching point. On one side of the main-axis, viewed anteriorly, this is in the extreme right position; on the other side of the main-axis, this is in the extreme left. In each case, the other two positions are replaced by a pinnate terminal kenozooid group. The stolons along a lateral side branch are thus deflected anteriorly at each junction, in relation to the main-axis stolons. The branches therefore form inward facing arches across the anterior surface of the main-axis stolons. The resulting form is a long 'cylindrical' plume, reminiscent of snake vertebrae with ribs. The colony is composed of a number of these plumes, arising from various positions. Autozooid groups occur towards the distal ends of stolons. In the main-axis stolons, there is a further, distal, autozooid-free portion to each stolon, usually corresponding in length to the width of a daughter stolon. In the side branches, the autozooids frequently overlap the subsequent branching point. All stolons may be curved anteriorly. Autozooids are outer-wall thickened, but the thickening differential is usually low. Autozooid group profile tends to be level. The arrangement of autozooids in groups along main-axis stolons is, to some extent, predictable. A proximal-most autozooid may be evident in a group, and is associated with one side of the stolon. This autozooid loses its prominence over the next few stolons, the proximal autozoids of the groups appearing equally paired. Eventually, a proximal-most autozooid becomes prominent once more, but this time is associated with the opposite side of its stolon. Such a sequence is estimated to occur over 5 stolon units. The original condition is regained after a sequence of 10 stolon units. Side branches, where produced, have autozooid groups each with a prominent proximal-most autozooid associated with the side of its stolon nearest the main-axis stolons. This arrangement is preserved in subsequent autozooid groups along a side branch, unless a main-axis sequence is produced. Rhizoids may develop, one per stolon, from the proximal most end of, usually, main-axis stolons. Each rhizoid is produced at about 30 deg. to the orientation of the autozooids on the same stolon.

Sl. (a) 2·44 Z/S. (a) 50%
Zn. (a) (14–25 (appearing as 7–12 'pairs')

Sl. (b) 1·60 Z/S. (b) 80%
Zn. (b) 18–28 (appearing as 9–14 'pairs')

Sl. (c) 1·13 Z/S. (c) 80%
Zn. (c) 18–28 (appearing as 9–14 'pairs').

Sd. 0·35 (all stolons)
Zh. 0·35 (all stolons)
Zw. 0·13 (all stolons)

REMARKS. The cuticle in some specimens is seen to bear numerous cyst-like bodies, whose structure and function have yet to be determined. These cysts appear to be associated with the distal, astogenetically later (most recently budded) parts of the colony.

The branching pattern and resulting shapes in parts of the colony are quite distinct. The overall result is that autozooids face into a relatively sheltered colony-bounded space. This arrangement may have some protective advantage (see page 341).

D'Hondt (1983) places *A. verticillata* Waters MS and *A. delicatissima* Busk MS in synonymy with *A. wilsoni*. Only the latter assertion is completely correct. The only apparent record of *A. verticillata* MS is of slide MM 7137, bearing the legend 'so named by Kirkpatrick . . . KP. afterwards called it *Amathia wilsoni* K'. *A. verticillata* is, thus, merely Kirkpatrick's MS name for what he subsequently described as *A. wilsoni*. The slide was part of Water's collection, from which the confusion probably arises. There appears to be no other record of *A. verticillata* Waters MS.

In the original description by Kirkpatrick (1888), a BMNH specimen from Port Jackson is apparently indicated. No such specimen has been found. The entry in the account is somewhat anomalous, in that the account deals with 'Polyzoa from Port Phillip'. It seems likely that Kirkpatrick was referring to an additional specimen, then held in the collections at the BMNH, but whose whereabouts cannot now be determined, simply of the same identity as that which he described. At the beginning of the account, Kirkpartrick stated that he was describing new species from a collection made by J. B. Wilson from Port Phillip, subsequently sent to the BMNH. Specimen BMNH 1888.5.17.7 matches this description in being part of such a collection, and is indicated as type material in catalogue and registration records, in Kirkpatrick's own hand. This specimen is clearly syntype material.

DISTRIBUTION. The species is known from the south-eastern region of Australia, ranging from Holdfast Bay near Adelaide to Port Jackson near Sydney and Hobart, Tasmania. The record from Flinders Island is not clear; it could refer to the island off Tasmania or that in the Great Australian Bight.

Amathia pinnata Kirkpatrick, 1888

(Figs 3B, 10A, B)

Amathia pinnata Kirkpatrick, 1888: 19, pl. 2 (figs 5, 5a).
Amathia pinnata: MacGillivray, 1895: 136, pl. C (figs 1, 1a).
Part *Amathia pinnata*: d'Hondt, 1979: 16.
Part *Amathia inarmata*: d'Hondt, 1983: 67, fig. 36 (G).
Not *Amathia inarmata*: d'Hondt, 1983: 67, pl. 2 (fig. 1) (= *A. biseriata*).

MATERIAL EXAMINED

Lectotype (selected here): BMNH; 1888.5.17.8 A, Port Phillip, J. B. Wilson Collection.
Paralectotypes: BMNH; 1888.5.17.8 B, C, Port Phillip, J. B. Wilson Collection.

OTHER MATERIAL

BMNH; 1847.6.23.14, Tasmania. 1884.11.14.5–12 B, Port Phillip. 1886.6.8.1, Griffths Point, Port Jackson. 1963.2.12.363, George Town, ?Tasmania? 1985.3.28.1, Port Phillip Heads, 15 m. 1985.3.30.2, Algoa Bay, S. Africa.

MM; 7109/2W, Port Phillip.

DESCRIPTION. In the erect part of the colony, branching is regular and almost always trifurcate. This results in a typically compound pinnate arrangement. At any branching point, one daughter stolon is produced in rectilinear succession, and two others are produced laterally opposing, at an angle of about 60 deg. to the centre. Stolons tend to be straight. Autozooids are distally located, occupying the greater part of stolons. Autozooid groups develop as far as the subsequent branching point, but do not overlie it. Autozooid group profile tends to be level, and autozooids are outer-wall thickened, although there is a tendency for both differential and overall thickening, not to be great. Autozooid group orientation from stolon to stolon is generally well preserved. The arrangement of autozooids on stolons lying in rectilinear succession is to some extent predictable. Viewed anteriorly, a proximal-most autozooid may be prominent in an autozooid group, and is associated with one side of the stolon. Over successive stolon units, each autozooid group shows rearrangement so that this autozooid loses prominence. The proximal autozooids thus appear equally paired, until a proximal-most autozooid becomes prominent once more, this time associated with the opposite side of the stolon. Such a series appears to occur over a sequence of 4 stolon units. The original condition is recovered on the seventh or eighth stolon unit. In lateral daughter stolons, a single proximal-most autozooid is prominent in the autozooid group, this being associated with the side of the stolon nearest the rectilinear series, i.e. for a right-branched stolon, the proximal-most autozooid is nearest the left side of its stolon, and vice versa. Autozooid groups on stolons subsequently produced from a lateral daughter stolon, display the same organisation along resultant rectilinear series and lateral components. Terminal lanceolate processes may occasionally be produced; each one is made up of a tapering series of three kenozooidal sub-units. These terminal lanceolate processes are usually produced simultaneously as a group of three, each process replacing a normal stolon. Rhizoids may be produced, approximately mid-way along the proximal autozooid-free part of the stolon. These arise singly or as a pair, one on either side of the stolon, at about 30 deg. to the autozooid orientation. Colonies may be large and arborescent.

Zh. 0·45 Z/S. 80%
Zw. 0·13 Zn. 18–49 (appearing as 9–24 'pairs')
Sl. 1·50–3.25 Tpl. 1·50
Sd. 0·35 (just proximal to the autozooid group)

Remarks. Measurements of this species given by Kirkpatrick (1888) appear to originate from the same material as he figured. There is, however, some discrepancy between the figures and the description, as it is possible to infer 18 autozooid 'pairs' from his figure, whereas he described the range as being from '12-16'.

Kirkpatrick's figure corresponds to a specimen which is obviously a fragment from a larger colony. However, this specimen and another which greatly resembles it, are obviously not from other material stored in the same container and bearing the same registration number. All these specimens are Kirkpatrick's *A. pinnata*, as is borne out by catalogue and registration records in Kirpatrick's own hand. There is a suggestion, in the stolon shape and rhizoid production site, that the registration may harbour two species. *A. pinnata sensu stricto*, is taken as the morph which corresponds with Kirkpatrick's figure; the registration of these components receiving the suffixes A and B (the remaining component the suffix C). Component A is the figured specimen, and is here designated the lectotype, the remaining portions, B and C, being paralectotypes. Provisionally, all three components are accepted as being *A. pinnata*.

This species is one of a number that were considered by d'Hondt (1979, 1983) to be synonymous with one another, the grouping also including: *A. biseriata*; *A. tricornis* (part); *A. brongniartii*; *A. cygnea* MS; *A. 'polycistica'* MS; *A. desmarestii* MS (see page 331). D'Hondt (1979) indicated *A. pinnata* Kirkpatrick 1888, as the senior synonym of this group. D'Hondt (1983) then indicates that *A. inarmata* MacGillivray 1887, is the senior synonym of the same compositional group, thus subordinating *A. pinnata* as a junior subjective synonym. *A. pinnata* is in fact not synonymous with any of the species in this grouping, being a separate and distinct species (see pages 332, 333).

Distribution. The species is known from the south-eastern region of Australia, ranging from Port Jackson, to Port Phillip Heads and Tasmania, also being recorded from Algoa Bay, South Africa.

Amathia biseriata Krauss, 1837
(Figs 4B, 11C, D)

Amathia biseriata Krauss, 1837: 23, fig. 1 (a, b, c).
Not *Amathia biseriata*: Busk, 1852: 385.
? *Amathella biserialis* Gray 1858: 320 (? errorum pro *Amathia biseriata* Krauss, 1837).

Amathella uniserialis Gray, 1858: 320.
Amathia inarmata MacGillivray, 1887: 183.
Amathia biseriata: Kirkpatrick, 1888: 17.
Amathia inarmata: MacGillivray 1889: 309, pl. 183 (fig. 4).
Amathia biseriata: MacGillivray, 1895: 137, pl. B (fig. 4).
part *Amathia pinnata*: d'Hondt, 1979: 16.
part *Amathia inarmata*: d'Hondt, 1983: 67, fig. 36 (G).

MATERIAL EXAMINED

Neotype (selected here): BMNH; 1887.12.10.90, Port Phillip, J. B. Wilson collection.

OTHER MATERIAL

BMNH; 1899.7.1.4317, 4318, 1963.2.12.357, Australia. 1899.7.1.4319, New Zealand. 1965.8.12.19, Jervis Bay, Huskisson, N.S.W. 1985.3.14.1, no locality.

NMV; H492 (1–9), Port Phillip Heads.

RM; 1808, Port Natal, Africa.

DESCRIPTION. In the erect part of the colony, branching is always bifurcate. Viewed anteriorly, at each branching point, one daughter stolon tends to lie approximately in line with the maternal stolon, although deviations of up to 20 deg. may occur. The other daughter stolon is usually produced laterally, at an approximate angle of 45 deg. to the main axis of the maternal stolon. The side on which a lateral branch appears, alternates at each successive bifurcation. Stolons have a slight constriction near the proximal end and are usually curved anteriorly, the curvature becoming progressively more acute distally, to bend around the distal end of the autozooid groups. The stolon tends to remain in contact with the distal side of the autozooids. Where this is not so, this portion of the stolon remains autozooid-free. Daughter stolons produced in the 'linear' position, arise from the distal end of the maternal stolon; lateral daughter stolons are produced from the most sharply curved region of the maternal stolon. The distal region of the maternal stolon may show some axial subdivision to bear the daughter stolons, more so when it is not in contact with the distal face of the autozooids. Autozooid groups on maternal stolons are rarely developed distal to the origin of the lateral daughter stolon, or where the stolon shows division. Autozooids are outer-wall thickened, the thickening sometimes being accentuated at the rims. Autozooid group profile appears level, sometimes slightly concave centrally, or diminishing slightly proximodistally along the stolon. A single proximal-most autozooid is evident in each group, slightly broader than the rest, usually placed just off the mid-line, and thus associated with one or other side of the stolon. No pattern has been discerned in the location of this autozooid from stolon to stolon. Sometimes both daughter stolons show the same autozooid arrangement as on their maternal stolon; sometimes the opposite; sometimes combinations of the two. Autozooid orientation is generally well preserved from stolon to stolon. Rhizoids may be produced, one per stolon, arising from a position level with, or just proximal to, the proximal-most autozooid of the autozooid group. The orientation of the rhizoids is between 90–135 deg. to the autozooid group, occurring on the same side of the stolon as the direction in which that stolon was budded. Stolons and their autozooid groups become shorter nearer the distal (astogenetically later i.e. most recently budded) regions of the colony.

Sl.	2·05	Z/S.	75%
Sd.	0·32	Zn.	5–25 (appearing as 4–12 'pairs')
Zh.	0·35		
Zw.	0·11		

REMARKS. The autozooid pattern from stolon to stolon remains elusive in this species, primarily due to the difficulties of observation over the number of stolon sequences necessary.

This species is one of a number that were considered by d'Hondt to be synonymous with one another. D'Hondt (1979) indicated that *A. pinnata* Kirkpatrick 1888, was the senior synonym of this group, inclusive of *A. biseriata*, and then (1983) indicated that *A. inarmata* MacGillivray 1887 was the senior synonym of the same compositional group. Both assertions are erroneous. The inclusion of the name *A. desmarestii* in this group is of little consequence as Lesueur never published his work. The name itself is not valid in being published only in synonymy (I.C.Z.N. article 11e). Of the other species in this group: *A. tricornis* is a separate and distinct species (see page 321), with a more complex colony composition than the rest; *A. cygnea* Busk MS, and *A. polycistica* (sic) Busk MS, are here considered to be synonymous with one another as *A. brongniartii* (see page 333); *A. pinnata* is also a separate and distinct species, in which trifurcate branching predominates. There are no indications, in any of MacGillivray's accounts of *A. biseriata*, of the trifurcate branching pattern shown by d'Hondt (1983), who reproduced MacGillivray's (1895) figure of *A. pinnata*. In fact, MacGillivray and Krauss both stated that the branching pattern in *A. biseriata* is dichotomous. Supplementary features which may be used to distinguish between *A. biseriata* and *A. pinnata* are: the site of rhizoid production; the occurrence of terminal kenozooids in the latter species. Were *A. biseriata* and *A. pinnata* synonymous, then *A. biseriata* would be the senior synonym (cf. d'Hondt 1979). *A. biseriata* however, is synonymous with *A. inarmata*, but again, it is *A. biseriata* which is the senior synonym. In this case, Krauss' publication predates that of MacGillivray by 50 years. Furthermore, MacGillivray (1895) accepted his species to have been the same as that of Krauss. MacGillivray's syntypes are held in the NMV (H492 1–9), and all 9 specimens are *A. biseriata*.

MacGillivray (1895) appears to have been under the misconception that Krauss' material of *A. biseriata* originated from south Africa, when in fact it was from New Holland i.e. western Australia. It is probable that MacGillivray (1895) was actually referring to material received from 'Pergens' (MacGillivray, 1889).

Krauss' (1837) description and figures are here considered to be more than adequate to distinguish his species from any other; his only mistake was to make the assumption that the rhizoids produced the stolons and their autozooids. Krauss' material does not appear to have survived. In view of the subsequent confusion, selection of a neotype is necessary. BMNH 1887.12.10.90 (although from Port Phillip) is selected here.

DISTRIBUTION. The species is known from south Africa, southern Australia and New Zealand.

Amathia brongniartii Kirkpatrick, 1888
(Figs 4A, 11A, B)

Amathia brongniartii Kirkpatrick, 1888: 18, pl. 2 (figs 3, 3a).
Amathia brogniartii (sic): lapsus calami MacGillivray, 1895: 136, pl. B (figs 3, 3a).
Part *Amathia pinnata*: d'Hondt, 1979: 16.
Part *Amathia inarmata*: d'Hondt, 1983: 67.
Not Part *Amathia inarmata*: d'Hondt, 1983: 67, fig. 36G, (= *A. pinnata*).

MATERIAL EXAMINED

Neotype (selected here): BMNH; 1888.5.17.6, Port Phillip, J. B. Wilson Collection.

OTHER MATERIAL

BMNH; 1838.2.26.13, 1847.6.23.4, 1899.7.1.4379, 4381, Tasmania. 1887.4.27.19, Port Jackson, N.S.W. 1887.12.10.98A (part), Port Phillip, Vict. 1899.7.1.4419, 6601, Swan Is. ?Bass Strait? 1927.9.26.21, Swan Is., Banks Strait. 1984.12.4.1, Portsea Pier, Victoria, 2 m. 1985.3.16.1, Victoria. 1985.3.16.1.2a,b, Flinders Is. ?Tasmania?

NMV; 65397, Port Phillip Heads, Vict.

MM; 7074, Lane Cove, Port Jackson, N.S.W.

DESCRIPTION. In the erect part of the colony, branching is always bifurcate. At each branching point, one daughter stolon tends to continue in line with the maternal stolon, often giving rise to rectilinear series, although deviations by up to 15 deg. may occur. The other daughter stolon of each birfurcation arises laterally, often anterolaterally, appearing on alternate sides along a series, at an angle of between 20–50 deg. to the axis of the maternal stolon. Stolons are usually straight and tend to have a slight constriction near the proximal end. The distal end of a stolon does not usually show any axial subdivision or widening to bear daughter stolons; more often, the maternal stolon shows some abbreviation into a wedge shape to accommodate these. The autozooid groups develop as far as, and often overlie the subsequent branching point. Autozooids are markedly inner-wall thickened, with a thin walled exterior. The autozooids are usually, large, prismatic, and pentagonal in section. Viewed anteriorly, the walls between the autozooids, being much thicker, give a characteristic zig-zag backbone appearance to the autozooid groups. Autozooid group profile ranges from gently arched upwards to level with the autozooids shorter at each end of the group. A single proximal-most autozooid is evident in each autozooid group, slightly broader than the rest, usually just off the mid line and thus associated with one or other side of the stolon. Viewed anteriorly, this autozooid is always on the side nearest the sister stolon. Autozooid orientation from stolon to stolon is generally well preserved. Rhizoids may be produced, one per stolon, from a position level with or just proximal to the proximal-most autozooid of a group. These arise at about 110–160 deg. to the autozooid orientation on the same stolon, and on the same side of the stolon as the direction in which the stolon was budded. Stolons and their autozooid groups appear to be shorter nearer the distal (astogenetically newer) regions of the colony.

Sl. 1·75–4·00 Z/S. 80%
Sd. 0·25 Zn. 10–39 (appearing as 5–18 'pairs')
Zh. 0·48
Zw. 0·15

Remarks. This species was considered by d'Hondt to be a junior synonym of: (1979) *A. pinnata*; then (1983) of *A. inarmata*. *A. brongniartii* differs from *A. pinnata* in many features, such as: the autozooidal thickening; the sites of rhizoid production; the basic branching pattern. *A. inarmata* is itself a junior synonym of *A. biseriata* (see page 332). Kirkpatrick (1888) and MacGillivray (1895) indicated differences between *A. biseriata* and *A. brongniartii* in their accounts. The two species may be distinguished quite readily by: the shape of the stolons; to some extent, the site of rhizoid production; the autozooidal thickening, this last being the most prominent difference.

A. brongniartii appears to display a large variation in stolon length and attendant number of autozooids borne. Such variation may be seen within single colonies. However, colonies may often show good uniformity in stolon lengths, whether long, short or intermediate. Busk, in his unpublished notes and figures stored at the BMNH, considered the possibility that the extremes of the size range might be discrete. He appears to have called colonies with short stolons and lower autozooid number *A. cygnea* (up to 20 autozooids, equivalent to 8–12 'pairs'), with more diminutive versions as *A. cygnea var. nana*. Colonies with higher numbers of autozooids (24–36 units, equivalent to 12–18 'pairs') and longer stolons, he called *A. polycystica*. In Busk's material, the specimens which might be *A. polycystica* tend to be dark coloured, but other than this there seems to be nothing which distinguishes them taxonomically. (Busk's notes make no recognition of the *A. brongniartii* in the unpublished plates of Lesueur).

Kirkpatrick (1888), in his account of *A. brongniartii*, erroneously credited the species to Desmarest and Lesueur, citing Lesueur's figures and Pergens' (1887) collations as his reference for the identity and name. As Desmarest and Lesueur never published their work, the Pergens mentions the name only in synonymy, Kirkpatrick is the authority for the species (I.C.Z.N. article 11e). As Kirkpartick did not consider himself the author of the species, he did not choose any type specimens. Kirkpatrick's figures, like those of Lesueur, are of insufficient quality to be utilised as reliable references. Kirkpatrick's figures hardly show any detail at all, whilst Lesueur's figures (pl. 13 fig. 5) show curved stolons and tube-like autozooid anteriors, both characteristics of *A. biseriata*. At the same time however, Lesueur shows approximately 20 'pairs' of autozooids, a number high enough to be associated with *A. brongniartii*. Understandably, confusion has arisen and so it would seem appropriate that a neotype be designated. BMNH 1888.5.17.6 is, therefore, selected as neotype. This specimen is the only one labelled as *A. brongniartii* by Kirkpatrick in the collection made by J. B. Wilson from Port Phillip. This collection is the subject of Kirkpatrick's publication of 1888.

Specimen NMV 65397 is believed to have been before MacGillivray at the time of his writing his 1895 account of *Amathia* species (in litt. NMV. 30th May 1983.). The specimen is undoubtedly *A. brongniartii* Kirkpatrick, thus MacGillivray's name 'A. brogniartii' is simply a misspelling, as his synonymy indicates.

Distribution. The species is known from south-eastern Australia, ranging from Tasmania to Port Jackson.

Amathia alternata Lamouroux, 1816
(Figs 4C, 13A, B)

Amathia alternata Lamouroux, 1816: 160.
Amathia alternata: Lamouroux, 1821: 10, pl. 65 (figs 18, 19).
Amathia alternata: Lamouroux, 1824: 44.
Not *Amathia alternata*: Osburn, 1932: 444, pl. 1 (fig. 4).
Part *Amathia convoluta*: Maturo, 1957: 22, fig. 11.
Not part *Amathia convoluta*: Maturo, 1957: 22, fig. 10.
Amathia alternata: Winston, 1982: 108, fig. 8.

MATERIAL EXAMINED

Neotype (selected here): USNM; 6307 (part), Albatross Stn. 2619, off Cape Fear, North Carolina.

OTHER MATERIAL

BMNH; 1964.7.10.1A,B, New River Inlet, North Carolina.
1964.7.10.2, Alligator Harbour, North Carolina.

DESCRIPTION. In the erect part of the colony, branching is always bifurcate. At each branching point, one daughter stolon tends to continue in line with the maternal stolon, forming a linear series. The other daughter stolon is produced at approximately 45 deg. to the maternal stolon axis at that location, at between 45–90 deg. to the orientation of the distal autozooids there. Branching may appear equally dichotomous at times. Daughter stolons are produced from the posterior side of the maternal stolon, this showing some abbreviation into a wedge shape to accommodate them. Stolons are: narrowed proximally, additionally having a proximal constriction; often curved posteriorly, also undergoing a slight twist along their length. The linearly disposed stolons may thus appear as an undulating progression. Any twist in these is normally reflected in the autozooids borne, changing the orientation between proximal and distal autozooids in a group by up to 90 deg. At times, this may give the impression that autozooid groups are simply arranged obliquely on the stolons. Autozooid groups may, however, be arranged along the stolonal axis without any evidence of twist at all in either component. Where the twist, proximodistally along a stolon, is clockwise, the left daughter stolon is produced in the 'lateral' position, and with anticlockwise twist, the right. The direction of twist is generally well preserved from stolon to stolon (although both directions may be found in the same colony). Lateral daughter stolons are thus produced from the same side of stolons along any linear sequence. The spatial orientation of these lateral branches is determined by the maternal axis and autozooid orientation at that point. Autozooid orientation changes by 100–180 deg. from stolon to stolon. This is taken from the distal autozooids on the maternal stolon to the proximal autozooids on each of the two daughters. Autozooids frequently overlie the subsequent branching point and are outer-wall thickened. Autozooids are inclined at about 60 deg. to the stolonal axis, and group profile is level or gently convex. A proximal-most autozooid is frequently evident in each group. Viewed anteriorly, this is associated with the side of the stolon in which the direction of twist occurs e.g. the right side, with clockwise twist proximodistally. Rhizoids may be produced at any point on a stolon from the constriction to beneath the proximal autozooids. A polyrhizoid condition may result, where any number of rhizoids, up to a maximum of 5, possibly more, may be produced from a single stolon, at any orientation. Two orientations appear more frequently occupied by rhizoids: within 10 deg. of the proximal autozooid orientation on the same stolon; approximately 180 deg. to the proximal autozooid orientation.

Zh.	0·42	Z/S. 85%
Zw.	0·10	Zn. 24–57 (appearing as 12–28 'pairs')
Sl.	1·45–3·87	
Sd.	0·29–0·35 (just proximal to the autozooid group)	

REMARKS. In the non-erect part of the colony, secondary thickening of stolons may occur. This has the appearance of a sleeve developing along existing stolons.

A. alternata can display a consistent, if only slight, spiral nature, and the species has been confused with *A. convoluta sensu* Lamouroux, and possibly also with *A. semiconvoluta*

Lamouroux. As no type material exists, it may also be possible to confuse *A. alternata* with other spiral-autozooid group species, for example *A. tortuosa* Tennison Woods or *A. connexa* Busk.

Maturo (1957) described and gave representative figures, under the name of *A. convoluta* (*sensu* Lamouroux), of material collected at Fort Macon on Bogue Banks, USA. This material was noted to have 'straight autozooid groups, alternately placed from one internode to the next', and to be the same as a specimen in the USNM labelled *A. spiralis*, from Albatross Stn. 2619, off Cape Fear, North Carolina. The latter, USNM 6307 (part), has been examined here. Portions of this specimen have autozooids arranged and placed in the way Maturo describes and illustrates for the Fort Macon material. This specimen, Maturo's account, and the description given here, conform with Lamouroux's brief description of *A. alternata* in 1816, his subsequent account of 1821, in which he presents figures (pl. 65, figs 18, 19), and his final account in 1824.

Lamouroux's (1821) figures lack important information, and, in not being published at the same time as the original description, are clearly not eligible for any type status. Lamouroux's collection was destroyed during the Second World War (d'Hondt in litt. 27.10.1982), but material from his collection obtained via Busk, and labelled *A. alternata* is stored at the BMNH as 1897.7.1.6606. This material was originally stored dried and pressed, but has subsequently been rehydrated, and is at present stored in alcohol. As recorded on a label with the material, examination by Dr F. Maturo before rehydration revealed only two bryozoan species, these being other than *A. alternata*, possibly *A. brasiliensis* Busk and *Zoobotryon verticillatum*. Since rehydration, the absence of *A. alternata* is here confirmed, and the identity of the two other species established as *A. wilsoni* and *A. semiconvoluta*.

The packet originally enclosing the specimens bears the names 'A. alternata' and 'Amerique' in what is taken to be Lamouroux's handwriting. The locality mentioned does not disagree with that of Lamouroux's accounts (1816, 1821, 1824) of *A. alternata*, (the most specific locality given being the Sea of Antilles in 1824). The two species found enclosed in the packet, however, are not expected from this region; all other records of *A. wilsoni* are from southern Australia. Similarly, all other records for *A. semiconvoluta* are from the Mediterranean, the species possibly extending as far along the west African coast as Nigeria. It is unlikely that *A. wilsoni* would have been confused with *A. alternata* by Lamouroux, as the species has many distinguishing features and lacks alternate autozooid group placings. It may be possible to confuse dried *A. semiconvoluta* with *A. alternata*, but this is considered unlikely of Lamouroux, as he is the author of both species. Lamouroux introduced *A. alternata* in 1816, redescribed the species in 1821 and again in 1824 when he introduced *A. semiconvoluta*, the descriptions for the two species appearing on the same page. It is to be assumed that the author was capable of recognising and distinguishing his own species. The fate of any *A. alternata* that may have been present in BMNH 1897.7.1.6606 is open to speculation. The circumstances of Busk's acquisition of specimens enveloped in paper bearing Lamouroux's writing are unknown.

In the interests of nomenclatural stability, a neotype is required. Specimens considered eligible are: those in the BMNH under 1964 registrations, all from North Carolina, donated and identified by Dr F. Maturo as *A. alternata*; specimen USNM 6307 (part); Maturo's Fort Macon material. The whereabouts of the Fort Macon material (Maturo 1957) is not known. The neotype selected, therefore, is specimen USNM 6307 (part) from Cape Fear, off North Carolina, at 15 fthms. (27.43 m) this being the earliest recorded specimen surviving. The polyrhizoid condition is not readily apparent in this specimen, but it does show the possible variation in the arrangement of autozooid groups.

The difference between *A. alternata* and *A. semiconvoluta* are as follows: the degree of 'spirality' that may occur is much greater in *A. semiconvoluta* (180–270 deg., cf. *A. alternata* 0–90 deg.); the orientations of the distal end of one autozooid group and the proximal end of the next are within 10 deg. of each other in *A. semiconvoluta*, but a distinctive 100–180 deg. in *A. alternata*; a lower linear autozooid to stolon ratio of 50% for *A. semiconvoluta*, compared to about 85% in *A. alternata*. Although rhizoids may appear at similar orientations in both species, only *A. alternata* shows polyrhizoidy with rhizoids in proximity to the autozooids (and, additionally, a slightly wider bifurcation angle between daughter stolons). In *A. semiconvoluta* the rhizoids appear at the proximal-most end of the stolons, at about the same orientation at which the preceeding autozooid group terminates, or displaced by 180 deg., or when two rhizoids are present on the same stolon, at both orientations. *A. semiconvoluta* is understood from the following specimens: BMNH; 1885.12.5.12,13, Marseilles. 1888.11.9.4, Naples. 1899.5.1.290, 1912.12.21.687, Adriatic. 1899.7.1.6606pt., ?locality?

The other species mentioned above i.e. *A. convoluta*, *A. tortuosa* and *A. connexa*, are also distinguishable from *A. alternata* by their degree of spirality. This is significantly greater than *A. alternata* in all cases. Problems might arise, however, in distinguishing these three species from each other, and establishing their validity.

A. convoluta is understood from BMNH 1899.7.1.6607. This specimen is from Lamouroux's collection, obtained via Busk, and is labelled 'Amathia convoluta, Australasia' in what is accepted to be Lamouroux's handwriting. There is nothing to contradict its identity from any of Lamouroux's descriptions. The specimen also conforms with MacGillivray's (1895) account of the species, corroborated by his opinion on Busk 1884 (pl. 6. fig. 2, there misidentified as *A. spiralis*). However, there is nothing to suggest that MacGillivray ever saw BMNH 1899.7.1.6607 at any time. This specimen is noted as 'type' in the catalogue of the BMNH, though no formal declaration of its purported status has ever been made. It is possible that the specimen was formative of Lamouroux's opinions of the species and thus a 'type' but there can be no certain evidence for or against this notion. However, the specimen appears to be the only extant material which bears an unchallengeable identification, attributable to the original author. D'Hondt (1983) indicated that Lamarck's name for the species (*Amathia crispa*), as the senior synonym, should instead be used.

DISTRIBUTION.The species is recorded off North Carolina, USA, and, from Lamouroux's (1824) record, from the Caribbean.

Amathia pruvoti Calvet, 1911
(Fig. 13D)

Amathia pruvoti Calvet, 1911: 59, fig. 2.
Amathia pruvoti: Bobin & Prenant, 1956: 287, fig. 128.
Amathia pruvoti: d'Hondt, 1983: 67, fig. 35F.
Amathia pruvoti: Hayward, 1985: 136, figs 46A, B.

MATERIAL EXAMINED

Type: LBIMM; Bry 8205, Calvet collection: no locality.

OTHER MATERIAL

BMNH; 1882.7.7.1–2, Trieste. 1882.7.7.–, Mediterranean.
1885.12.5.14, Montpellier. 1889.7.27.48, 1890.7.22.8 part, Studland Bay, Dorset. 1975.7.1.15, Emborios Bay, Chios, 90 ft. 1984.2.26.102, Dhiaporia Rock, Chios, 100 ft.

DESCRIPTION. In the erect part of the colony, branching is always bifurcate. Daughter stolons appear to diverge equally, lying at approximately 60 deg. to each other, thus giving the impression of equal dichotomy. In fact, at each branching point, one stolon tends to be budded in a linear position and is subsequently deflected, whilst the other is produced laterally. The linearly disposed daughter stolon may be wider than its sister, with little deflection, at times giving a strong impression of rectilinear progression. In all stolons, there is a slight constriction near the proximal end. The distal end does not show any axial subdivision or widening to bear daughter stolons; however, it often shows some abbreviation into a wedge shape to accommodate these. Autozooid groups sometimes overlie the subsequent branching point. However, it is more usual for the autozooid group to only develop as far as the branching point, or, alternatively, 'stop short' and be followed by an autozooid-free portion of stolon, about the width of an autozooid in length. Stolons tend to be straight proximally although often slightly curved posteriorly and undergoing an axial twist in the region of the autozooids. The twist in the stolon is usually reflected in the autozooids borne, changing the plane of their orientation, between the proximal-most and distal-most autozooids, by approximately 90 deg. The plane in which the subsequent bifurcation occurs is also affected to the same degree. The twists are normally predictable. Viewed anteriorly, in the left-branched daughter stolon, the twist is usually clockwise in a proximodistal direction, and anticlockwise in a right-branched daughter. These twists generally occur irrespective of the twist which occurs in the maternal stolon. However, there can be variations to this. Occasionally, both daughters may twist in the same direction, this being opposite to that of their maternal stolon. Occasionally, the inverse to the normal condition occurs, where a left daughter twists anticlockwise and the corresponding right daughter twists clockwise. Autozooids are outer-wall thickened. Autozooid group profile, where discernible, is level proximally, diminishing distally, resulting from decreasing height and increasing distal inclination of the autozooids. A single proximal-most autozooid is evident in each autozooid group, usually off centre to the axis of the stolon. Viewed anteriorly, this autozooid is always associated with the same side of the stolon, as the direction in which the autozooid group twists, e.g. the right side, with clockwise twist proximodistally. Autozooid orientation from stolon to stolon, changes by 180 deg. between the distal autozooids of the maternal stolon and the proximal autozooids of each of the two daughter stolons. No rhizoids are known, and the erect part of the colony appears as a diffuse cotton-wool like mass. Sometimes, erect components of the colony come into contact with the substratum, and their characteristic stolonal shape is lost. These components do not bear autozooids; as stolonal kenozooids (see page 309), they become elongated and twisted, occasionally branching and producing clumps of flattened lateral processes. Further erect components may be produced at any time and these may resume the normal erect growth pattern.

Sl. 2.40–3.75	Z/S. 60%
Sd. 0·13–0·15	Zn. 21–31 (appearing as 10–15 'pairs')
Zh. 0·40	
Zw. 0·13	

REMARKS. Apart from the ancestrula, little is known of the non-erect portion of the colony. It is assumed that this would resemble the contact-modified erect stolons and their growth behaviour. No occurrence of two autozooid groups on the same stolon has been encountered in any of the material examined (cf. Calvet, 1911). Such an instance would be contrary to the present concept of the genus.

There is a specimen at the LBIMM, bry 8205, originating from the Station Zoologique de Cette, Université de Montpellier. This is latterly documented (e.g. LBIMM loan form 26th Oct 1983) as 'the probable type of *A. pruvoti*: Calvet (Cette), with a handwritten label of the author carrying the name *A. semiconvoluta*'. The justification for regarding LBIMM bry 8205 as the type specimen of *A. pruvoti* Calvet, is not given. The specimen is, however, well preserved, and would serve as an excellent basis on which to recognise the species in future. It is proposed here that the specimen be accepted as the type specimen of the species. If no historical justification for its claimed status as a 'type' is available (see below), it is here selected as neotype, obviating the confusion that has arisen between *A. pruvoti* and *A. lendigera* (*sensu lato*).

It should be noted that there is some difference between Calvet's description (1911) and specimens subsequently recognised as *A. pruvoti*, including specimen LBIMM bry 8205. Calvet described stolons as lying in rectilinear series. This condition is not readily apparent in the majority of specimens, except in two specimens from Chios, BMNH 1975.7.1.15, 1984.2.26.102, and in these there is also little evidence of the proximal stolonal constriction. It is not possible to be certain of what Calvet meant when he described the 'stature' of *A. pruvoti* as 'erect', then drawing a comparative difference between it and *A. lendigera*, when the colony budding patterns of the two species are in fact very similar. It is possible that the supposed distinction may reflect an opinion that *A. lendigera* has a higher proportion of the non-erect colony component, or that the erect part of *A. lendigera* tends to be spatially more condensed. In both species, there is some variation in the overall length of stolons. This variation appears less extensive in *A. pruvoti*. The most obvious difference between the two species, however, lies in the disposition of autozooids about the stolons. A degree of twist is usually present in *A. pruvoti*, and an autozooid-free distal portion of the stolon often occurs.

Calvet also drew a comparison with *A. semiconvoluta*. The differences in the erect part of the colony between this species and *A. pruvoti* are that, in *A. semiconvoluta*: the curvature of the stolon beneath the autozooids is much shallower, if present at all; the autozooid height tends to be equal throughout the autozooid group; the autozooid group is more spiralled, undergoing twists of 180–270 deg.; the orientations of the distal end of the autozooid group on the preceeding stolon, and the proximal ends of the next, on the succeeding stolons, occur within 10 deg. to each other; the direction of spiral tends to be preserved from maternal to daughter stolons, although both directions may be found in the same colony; branching is always bifurcate (as in *A. pruvoti*) but one daughter stolon is always linearly disposed, giving rise to definite rectilinear series, with the other daughter stolon produced anterolaterally at about 30 deg. to the stolon axis and distal autozooid orientation; when the autozooid twist, proximodistally, is clockwise, the right hand daughter stolon is in the rectilinear position, and with anticlockwise twist, the left hand daughter stolon acquires the rectilinear position; autozooid groups always overlie the subsequent branching point; rhizoids are produced from the proximal end of stolons. Further characteristics of *A. semiconvoluta* are as follows: rhizoids arise singly, either in the same orientation as the proximal-most autozooids, or at 180 deg. to this (see pages 335, 336, Figs 5A, 13C); when two rhizoids per stolon are produced, these arise as one from each orientation; the production of rhizoids would enable the colony to attain an arborescent form, but this has not been confirmed.

There is, in addition, some similarity between *A. pruvoti*, *A. distans* Busk, *A. distans var. aegyptana* d'Hondt and *A. brasiliensis*, each of which is a distinct entity. The distinction between the species may be found in the following characteristics. In the last three, the autozooid groups are more spiral, usually describing a 360 deg. rotation about the stolon in *A. brasiliensis* and *A. distans*, slightly less (270–360 deg.) in *A. distans var. aegyptana*. Of this group, *A. brasiliensis* is the only one which produces rhizoids, these arising at the proximal end of stolons, orientated within 10 deg. to the proximal autozooids on the same stolon. *A. distans var. aegyptana* has the distinction of producing autozooid groups in which the direction of spirality remains preserved from maternal to daughter stolons i.e. all clockwise or all anticlockwise, whereas one of two other patterns prevail in *A. pruvoti*, *A. distans* and *A. brasiliensis*. Using the distal-most autozooids as the orientation reference, and viewing anteriorly: in *A. pruvoti* and *A. brasiliensis*, the left daughter stolons carry autozooids arranged clockwise in a proximodistal direction, and the right daughters, anticlockwise; in *A. distans*, the left daughter stolons carry autozooids arranged anticlockwise, and the right daughters, clockwise. The distinctions are made with reference to type material:

For *A. distans*: BMNH 1887.12.9.926, Bahia, 10–12 fthms. (18.29–36.58 m.).
For *A. brasiliensis*: BMNH 1887.12.9.927, Bahia, 10–20 fthms. (18.29–36.58 m.).
For *A. distans var. aegyptana*: BMNH 1926.9.6.25, Suez Canal.
For *A. pruvoti*: LBIMM bry 8205, no locality.

In conclusion, *A. distans var. aegyptana* should be considered as a species in its own right, and is here raised to specific rank as *Amathia aegyptana*.

Harmer (1915) drew attention to the similarities between *A. distans* and other species, including *A. pruvoti*. However, his understanding of *A. distans*, particularly in the degree of spirality which may occur, is here considered insufficiently rigorous. Unfortunately, it is Harmer's understanding which is followed by Bobin and Prenant (1956) and d'Hondt (1983).

DISTRIBUTION. The species is known mainly from the Mediterranean, with some material from Studland Bay in Dorset, England.

Discussion

It is readily apparent that there is a considerable degree of regularity and possible colony integration within species of the genus *Amathia*. Some of this is reflected in the consolidation of a colony by rhizoids. These grow back, sometimes fusing with each other, and ultimately interact with the substratum to provide support. The various arborescent growth forms that result can only be maintained through continued sustenance of these rhizoids, and of any underlying stolons which will usually have lost their feeding autozooids. This implies nutrient transfer to them, and thus a potential ability for self repair.

The most basic and obvious level of intergration, however, is the clustering of autozooids into groups on septa-bound kenozooidal stolons, to form intercommunicating functional units. These can show changes of characteristics with astogeny. Changes may be gradual, as in stolon lengths and autozooid numbers in *A. biseriata*; or discontinuous, as in the autozooid complement per stolon in parts of *A. tricornis*.

In the majority of cases, the polypide appears capable of retracting to about the level of the highest part of its associated thickened walls. This suggests that a degree of protection may be afforded by the thickening, and has some analogy to the situation found in other, calcified, bryozoans. It is not clear whether the mineral salts reported to be found in the body walls of *Amathia* (Ryland 1970) are associated with any particular feature, such as this autozooidal thickening.

From the autozooidal organisation evident, there are indications that some further analogy may be drawn between species of *Amathia* and other bryozoans, in terms of colony integration and co-ordinated behaviour. Together with regular budding patterns and specific orientations of autozooids, the localised autozooidal thickening carries with it implications for the achievement of lophophore eversion (and retraction). The thickened areas of cuticle might resist the deformation required by the autozooid to change its volume and effect these actions. There is little constraint on independent action of autozooids in those groups with inner wall thickening; the outer face of each autozooid is able to move freely in response to the volume changes necessary. In groups with outer wall thickening, the implied compliant boundaries for each autozooid are those walls contiguous with other autozooids. Thus, attempted changes in the colume of any one autozooid might impinge on the status of those adjacent. If these adjacent autozooids resist a change, then the eversion in the original autozooid will be hindered. It may be inferred, therefore, that in some species with outer wall thickening, feeding may be a group activity. Advantages of group feeding would lie in combined feeding currents, enhanced by specific autozooid orientations within colony bounded space, (Winston 1979, McKinney 1984). Independent autozooid behaviour is more likely if: the thickened outer wall has localised weak patches acting as diaphragms; the wall is sufficiently folded to allow concertina-like accommodation of volume change; the thickening differential is low; there are co-ordinated inverse volume changes of autozooid pairs. It cannot be discounted, however, that collective feeding may occur in either wall-type grouping, simply by co-operation of autozooids. Confirmation of possible patterns of feeding behaviour, however, requires the observation of living colonies.

In the autozooid groups, no pairing of autozooids may be confidently assigned throughout a colony in any species (see page 309). Although the concept of biserial rows loses some ground, it cannot be discounted completely. There is thus equal possibility that the arrangement of autozooids into groups may have evolved in any of three ways: by unification of two separate single rows of autozooids with subsequent modifications; by the linear organisation of randomly clumped autozooids; by spatial condensing, with alternate displacement, of one single row of autozooids. All three hypothetical initial conditions have some analogues in extant ctenostomes; the first in *Zoobotryon*, the last two in species of *Bowerbankia*. Tenuous indications for origins via the third category may be inferred from the order of autozooid production on stolons. Autozooids in a group are developed in distal sequence, often making their appearance laterally displaced on alternate sides. It is possible, however, that this simply reflects the fact that growth proceeds distally through a sequence of interlocked autozooids, as autozooids may also be seen to be produced as equal pairs.

As with many colonial organisms, a large epifauna is frequently associated with colonies of *Amathia*, presumably deriving benefit from the microenvironment of the colony interiors (see below). The colonies serve as a substratum for some organisms and as shelter for others. Great numbers of other bryozoans, coelenterates, crustaceans, annelids, algae, foraminifera and molluscs, are often found. In this context, the record of *Amathia* body walls containing calcium salts (Ryland 1970) needs re-investigation from material in which the absence of any encrusting calcareous epibionts is ensured, as these can be extremely diaphanous. It is not known if any of the associations are species-specific, or what other levels of interdependence may occur. The ecological criteria which determines distribution and survival of the species of *Amathia* are known in only most general terms, and nothing is known of the relative ecological requirements which epibionts and 'hosts' may have. All that might have been expected is that numbers of epibionts might be related to some simple factor, such as the degree of shelter a colony provides. However, Murray (1970) reported that the entire life-cycle of the gastropod *Marginella minutissima* is spent with Australian *A. biseriata*. In this case, the *Amathia* colony serves both as food substrate as well as the physical substratum. Murray's concluding suggestion was that it is the occurrence of the bryozoan which actually determines the mollusc's distribution.

The observable specific variation, and the limited numbers of recognisable characters perceived in these non-rigid animals, has made past workers, for example MacGillivray (1895), Hastings (1927), d'Hondt (1979, 1983), variably reluctant to accept the existence of certain species. As a result it has been suggested that some species, for example *A. lendigera* and *A. distans*, are almost ubiquitous. Wide geographic distributions, continuous or discontinuous, are not unknown amongst marine animals (Ekman 1967, Cook and Lagaaij 1973), and the genus has been reported from nearly all marine regions except the polar and subpolar seas. However, there is no evidence that any species of *Amathia* has ever achieved and maintained a cosmopolitan distribution. Any indications to the contary seem based on misidentifications. The problem is compounded in one instance; for two specimens, *A. wilsoni* and *A. semiconvoluta* ex Lamouroux collection (BMNH 1899.7.1.6606 parts), there is doubt that the locality data and specimens actually belong together (see page 335).

Although Rao and Ganapati (1975) reported '*Amathia distans*' as 'an important fouling species at the Visakhaptnam Harbour', species of *Amathia* are not noted as fouling the hulls of sea going vessels, and there is no indication that shipping has any effect (cf. Ryland 1970) on distribution. From the information available (albeit that this reflects the situation around the turn of the century, when many of the specimens studied were collected) the species determined appear to have distributions which reflect modern oceanic current flows (see below). This is not unexpected, as *Amathia* colonies are sessile, and the geographic distribution of species would be greatly dependent on dispersal of colony fragments and larvae by water currents.

Taken simplistically, the maintenance of widespread distributions suggests the need for adequate gene flow to help preserve the biological unity of each species (Sheppard 1975, Speiss 1977), and may be influenced by physical criteria. To some extent, this would involve the effects of sperm dispersal. Assuming some general similarity of ctenostomes with other Bryozoa, the free-swimming life of the lecithotrophic larvae (Barrois 1877, Nielsen 1971, Zimmer and Woollacott 1977), might be estimated at about 24 hours. Records of lecithotrophic larval life in Cheilostomata range from 20–75 minutes as in *Parmularia* (Cook and Chimonides 1985), to a maximum of 3–5 days as in *Crassimarginatella falcata* (Cook 1985). Under the same assumption of similarity, sperm life might be estimated as up to 1 hour (Marcus 1926 for *Electra pilosa*, Silén 1966 for *Electra posidoniae*). Lecithotrophic larval life in Bryozoa is generally held to be short and dispersal limited (Ryland 1976, Farmer 1977, Hayward and Cook 1983). Similarly, the contribution sperm dispersal makes towards preventing speciation must also be limited.

It is difficult to assess what contribution fragmentation makes towards species distribution; for the present, it is possible only to speculate on the effects of the factors involved. It is unlikely that colonies of *Amathia* would be susceptible to the same shear forces that might cause rigid, calcified colonies to fail structurally (Cheetham and Erikson 1983). The shape of *Amathia* colonies results partly from the exoskeletal function of locally thickened cuticles, but derives mainly from turgor pressure of the various coelomic fluids acting on the cuticles. The cuticles are flexible but non-elastic. Such an essentially hydrostatic support system would be capable of a great deal of deformation with subsequent recovery. Structural failure results when drag forces exceed tensile strength. Tensile strength of alcohol preserved specimens examined appeared subjectively high. The failure, near a bifurcation, of single stolons taken from distal tips of a specimen of *A. brongniartii* from Victoria Australia (BMNH 1984.12.4.1), was recorded at 80 grams.

Additional resistance to fragmentation is likely in colonies with dense branching. In these, water flow effects are prevented from acting directly on all the constituent components, and the effective drag of a colony is less than expected (Cheetham and Erikson 1983). Under this condition, much water flow would be redirected around the colony, and this would place some emphasis on the external hydrodynamic profile that a colony presents. A possible reaction to this is suggested in the fact that autozooids are often arranged to face into the relatively sheltered space within the colony interior, as for example in *A. wilsoni*, *A. woodsii*, *A. populea* and *A. guernseii.*

The characteristics of flexibility, reasonable tensile strength and hydrodynamic reaction are, however, the very features which have allowed *Amathia* species to spread into the kind of high energy environments, for example, much of southern Australia (Thomas and Shepherd 1982, King and Shepherd 1982) where, if only under severe storm conditions, fragmentation of colonies themselves must occur. In less extreme circumstances, for some species, fragmentation of the possible algal substratum might occur, setting entire colonies adrift.

The longevity of adult colony pieces, is potentially much greater than that of the larvae and sperm. Under laboratory conditions at the BMNH, specimens of *Flustrellidra hispida* survived for over 6 months without their original algal substratum, which had rotted away. The colonies adopted a highly mishaped globular form, approximately 1·5 cms. maximum dimension, lying free on the gravel filter bed of their container. These colonies could be bowled around by very mild water movement, while the great majority of the autozooids forming their surfaces, retained the ability to feed.

As colony fragments of *Amathia* do not readily float, it is to be expected that they will be transported well only whilst they are kept clear of the sea floor. Transportation and being kept clear of the sea floor will take place only as long as there is the appropriate energy in the water currents. More distant dispersal is possible if rafting on a more bouyant substratum, such as algae, occurs (Cheetham 1966, Cook and Lagaaij 1973). The success of any dispersals would require the eventual deposition of species in some suitable environment. Three levels of failure seem possible: that destination environments outside the recorded distribution are unsuitable (in which case, under certain circumstances, it is not impossible that remnants of at least some of these failures might be found); that dispersals do not reach wider transportation currents; that dispersals do reach wider transportation currents but suffer mortality en route, through loss of the 'raft' as the alga dies and rots. *A. lendigera* and *A. pruvoti* can be algal epibionts. These species, if any, would be expected to have achieved very wide distributions, but this does not appear to be the case. Their distributions instead appear similar to those of well documented Lusitanian faunas (Hardy 1959, Ekman 1967, Tait 1986, Currie 1983) (cf. *A. semiconvoluta* recorded from the west coast of Africa to the Mediterranean).

Regardless of the dispersal method of fragmentation products, direct survival of fragments would mainly be favoured by a low energy environment. Higher energy environments might allow survival only through subsequent release of larvae and their settlement. No colonies have been encountered where direct re-establishment of fragments is recognised to have occurred. It is quite possible, however, that colony fragments of variable size may re-attach and grow, and even that arborescent colonies resume their posture and growth form with the aid of rhizoids, in a process analogous to that observed in *Parmularia* (Cook and Chimonides 1985). However, whatever the frequency of fragmentation and outcome of subsequent events, the effects on distribution appear, for the present, to be of little significance.

The earliest record of fossil *Amathia* is from the Late Cretaceous, with a species appearing in the Maastrichtian of The Netherlands (Voigt 1972, Cheetham and Cook 1983). The genus is not associated with very deep water, the deepest record encountered being 150 fathoms (275 metres approx.) for specimens collected off Bahia during the Challenger Expedition. It seems likely, therefore, that the genus achieved its present day tropical to cold-temperate distribution via shelf waters through Tethys and the Tehuantepec Channel, and to have traversed these regions before their closure in the mid Miocene (Ekman 1967, Cook and Lagaaij 1973, Haq 1981). It is obvious that more evidence is required to support these suggestions, although this may not be readily available, as non-boring ctenostomes have a poor preservation record (Cheetham and Cook 1983).

It is interesting to note that some of the species recognised, *A. pinnata*, *A. woodsii*, *A. biseriata*, seem to have been recorded exclusively from both south Africa and southern Australia. Parallels exist for other bryozoan species (Hayward and Cook 1983). This distribution is almost certainly the resultant of palaeogeographic factors rather than of modern current flows (see below), and implies that the genus was established and speciated by the time Africa has moved into relative isolation from its Antarctic association. This does not extend the theoretical age of the group much beyond the Maastrichtian however (see above).

Although the imprecision of past records is criticized, the interpretation here of both *A. brongniartii* and *A. pinnata* from Australia, as two single species, rather than as species complexes, is prehaps lenient even on present evidence. Similarly, the specific genetic unity implied in each case for *A. biseriata*, *A. woodsii* and *A. pinnata* in both south Africa and southern Australia, although accepted here, must be viewed with caution. No linking distributions are recorded and gene flow through dispersal of sperm, larvae and colony fragments is not favoured over such distances and locations, and would not prevent divergence from occurring. Additionally, long term genetic stability of species is implied.

In general, it may be said that the members of the genus have had time to become distributed widely. There has also been enough time for the effects of isolation and isolating mechanisms in demes to have come into play (Schopf 1977, Speiss 1977). Furthermore, if the cryptic speciation indicated by Thorpe and Ryland (1979), for species of the ctenostome *Alcyonidium*, has any parallel in this ctenostome group, further subdivisions within many of the groupings proposed here should be expected.

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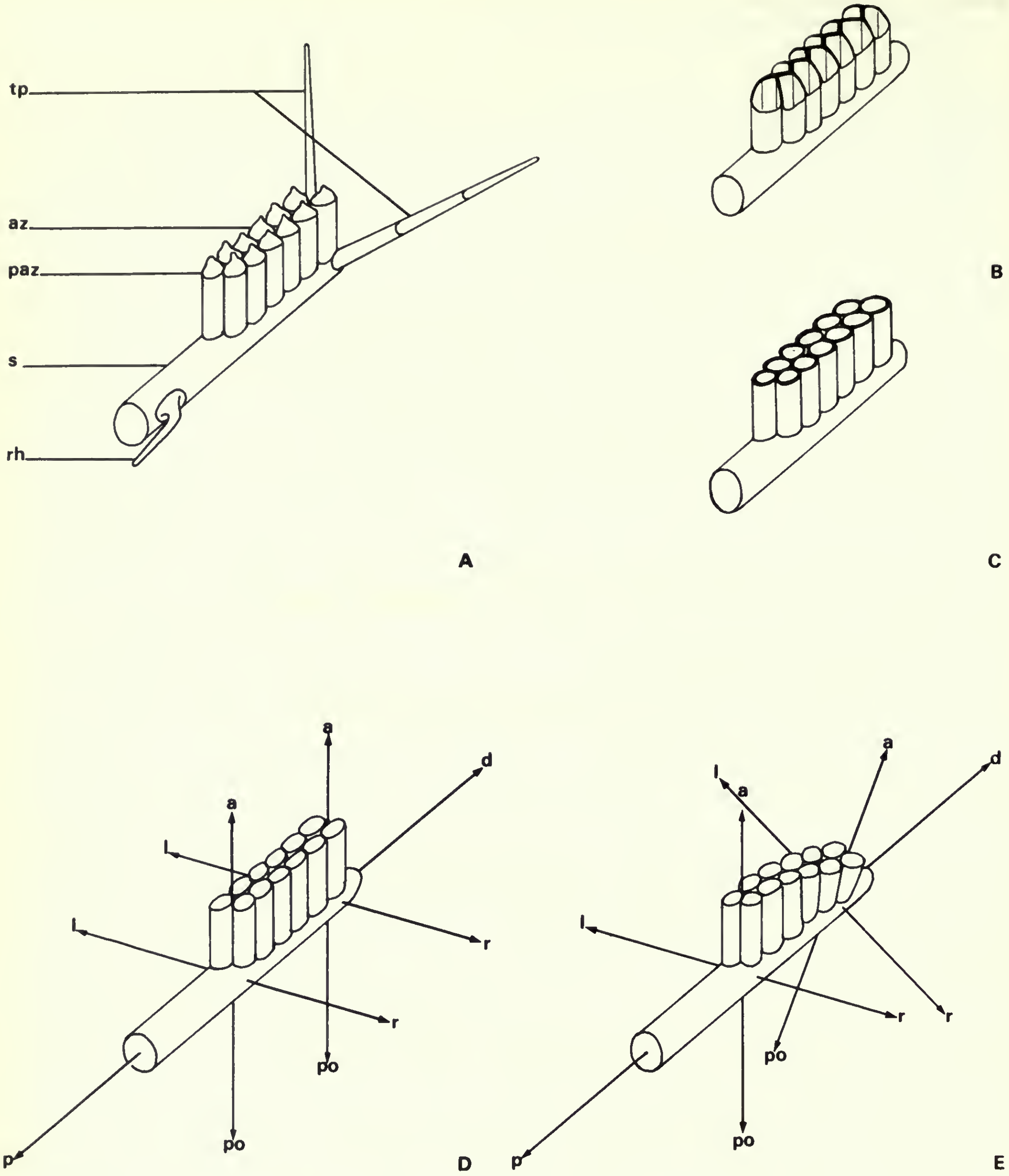
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Fig. 1 Schematic representation of erect colony components with reference orientations: (A) *az* autozooecia, *paz* proximal-most autozooid, *rh* rhizoid, *s* stolon, *tp* terminal process; (B.) interior wall thickening; (C.) exterior wall thickening; (D, E.) *a* anterior, *d* distal, *l* left lateral, *p* proximal, *po* posterior, *r* right lateral.

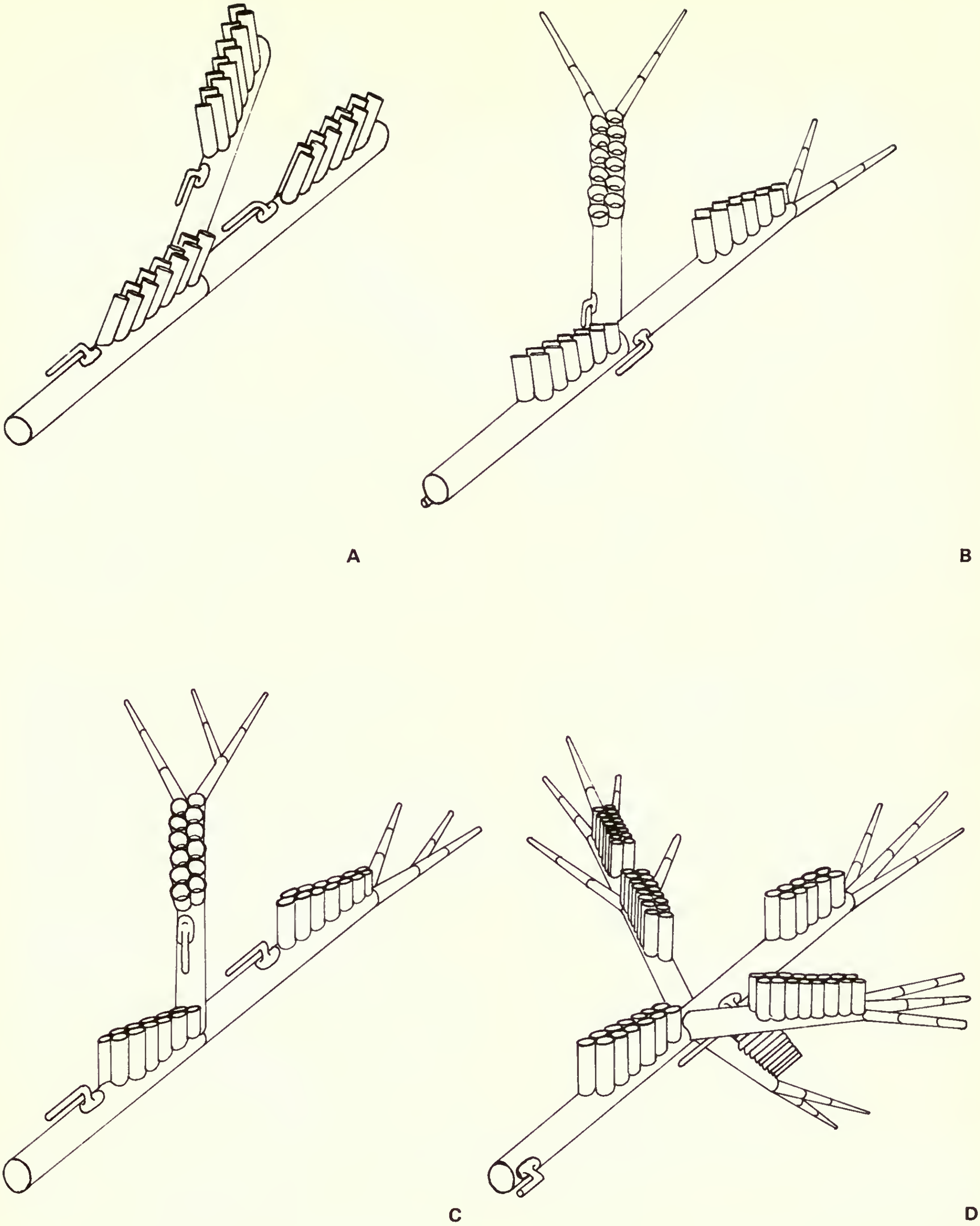

Fig. 2 Relative orientations of autozooecia and rhizoids about the stolon: (A.) *A. guernseii*; (B.) *A. populea*; (C.) *A. woodsii*; (D.) *A. tricornis*.

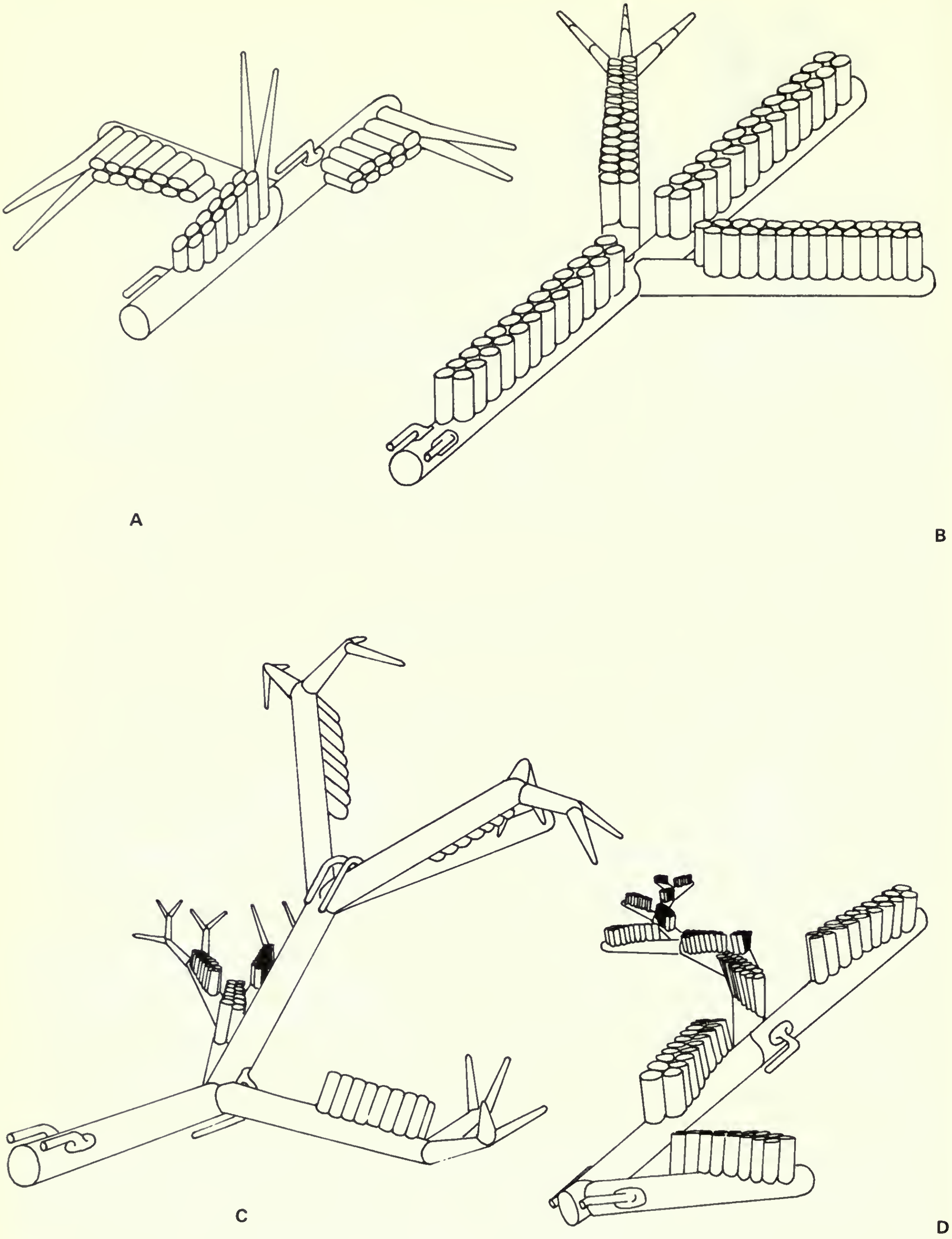

Fig. 3 Relative orientations of autozooecia and rhizoids about the stolon: (A.) *A. lamourouxi*; (B.) *A. pinnata*; (C.) *A. plumosa*; (D.) *A. obliqua*.

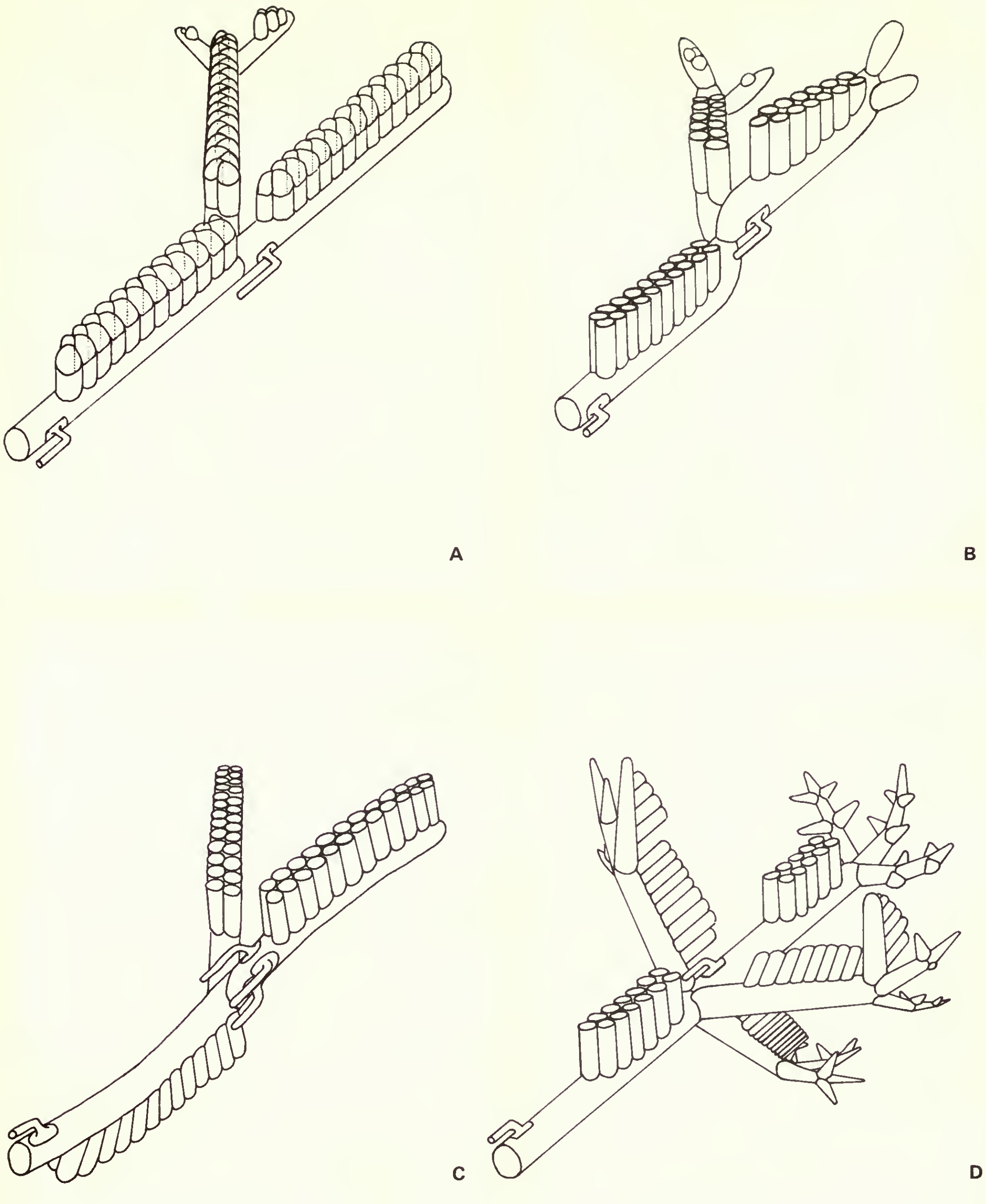

Fig. 4 Relative orientations of autozooecia and rhizoids about the stolon: (A.) *A. brongniartii*; (B.) *A. biseriata*; (C.) *A. alternata*; (D.) *A. wilsoni*.

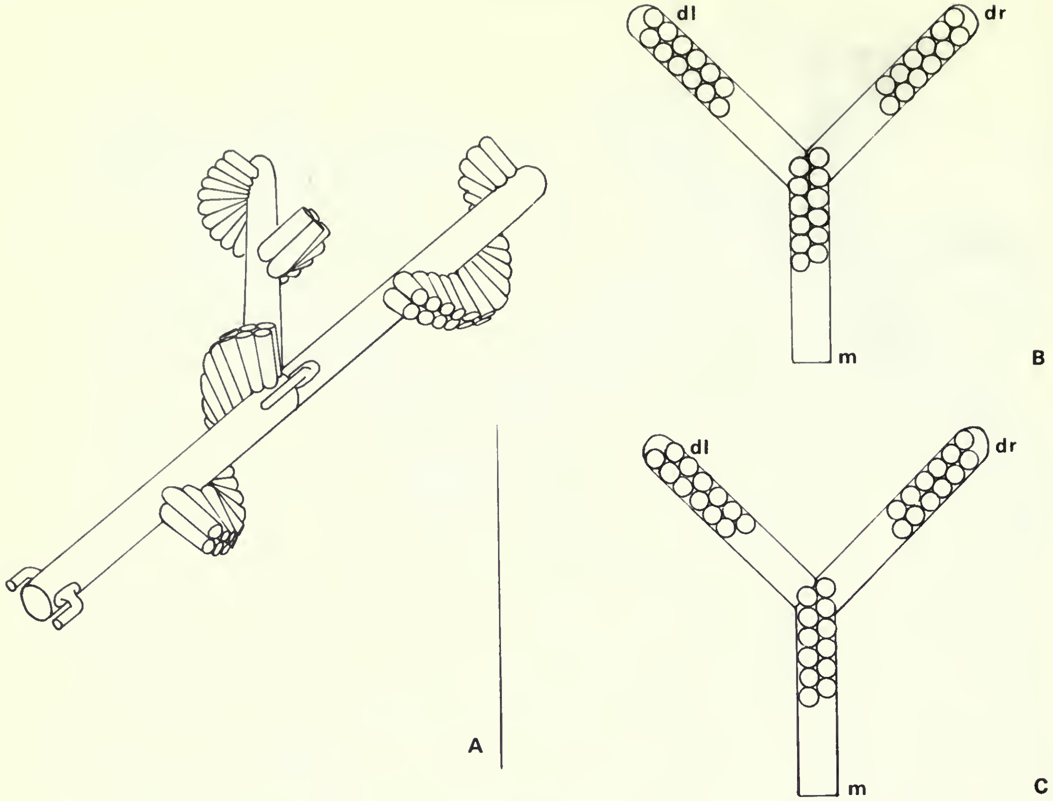

Fig. 5 (A.) Relative orientations of autozooecia and rhizoids about the stolon in *A. semiconvoluta*. Exemplified by *A. lendigera*: (B.) normal autozooid arrangement on a triad of maternal and daughter stolons with sister stolons carrying autozooid displacements to each other; (C.) alternative autozooid arrangement on a triad of maternal and daughter stolons, the daughter stolons carrying identical displacements, both opposite to the condition on the maternal stolon. *dl* left daughter stolon, *dr* right daughter stolon, *m* maternal stolon.

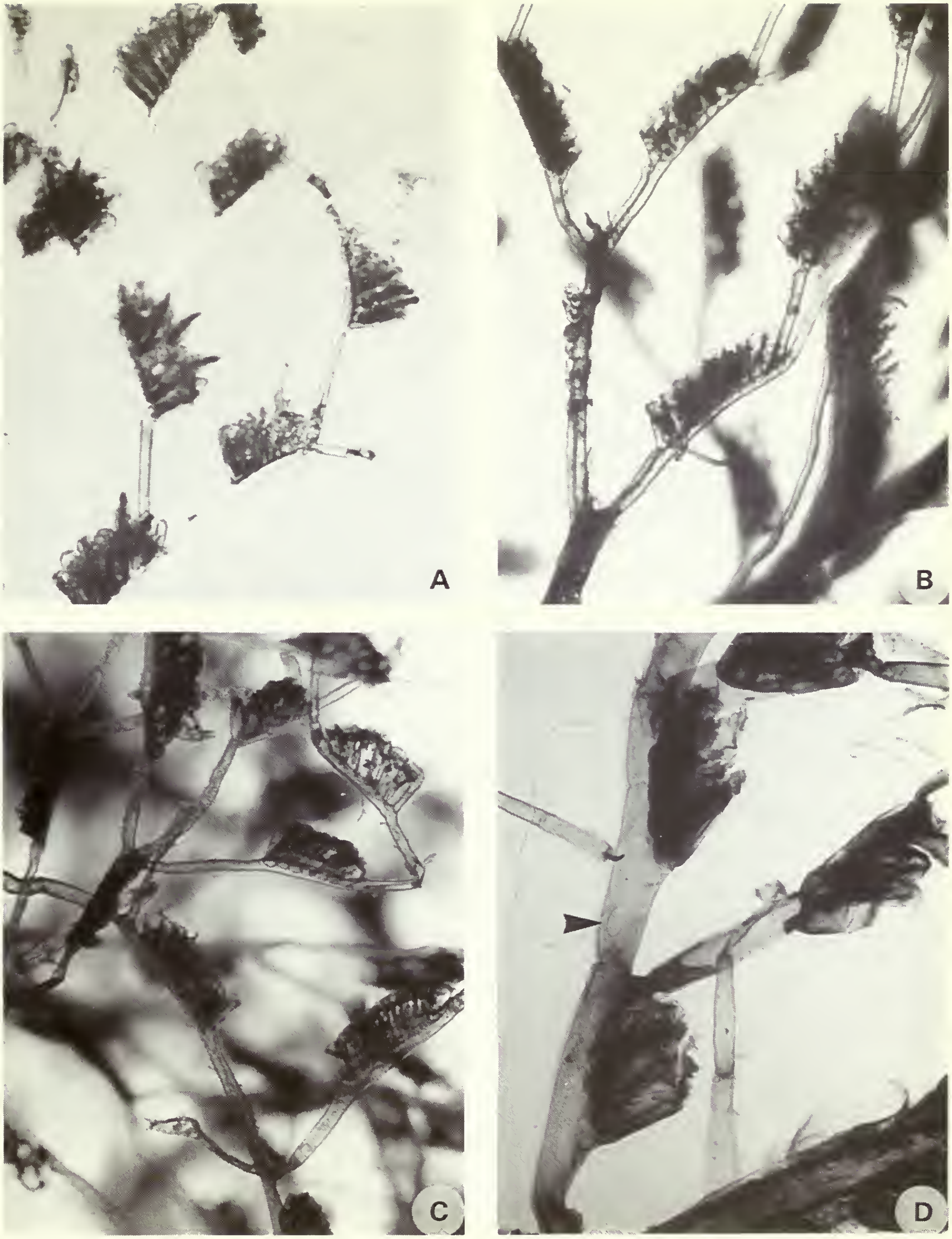

Fig. 6 (A.) *A. lendigera* BMNH 1942.8.6.15, Neotype, Chichester Harbour, UK. × 18; (B.) *A. guernseii* BMNH 1898.5.17.189, Holotype, Guernsey, *Guernsey*, UK × 17; (C.) *A. intermedis* BMNH 1887.5.2.18, Holotype, Hastings, UK × 27; (D.) *A. populea* BMNH 1899.7.1.526, Lectotype, Natal, South Africa, site of rhizoid origin arrowed × 44.

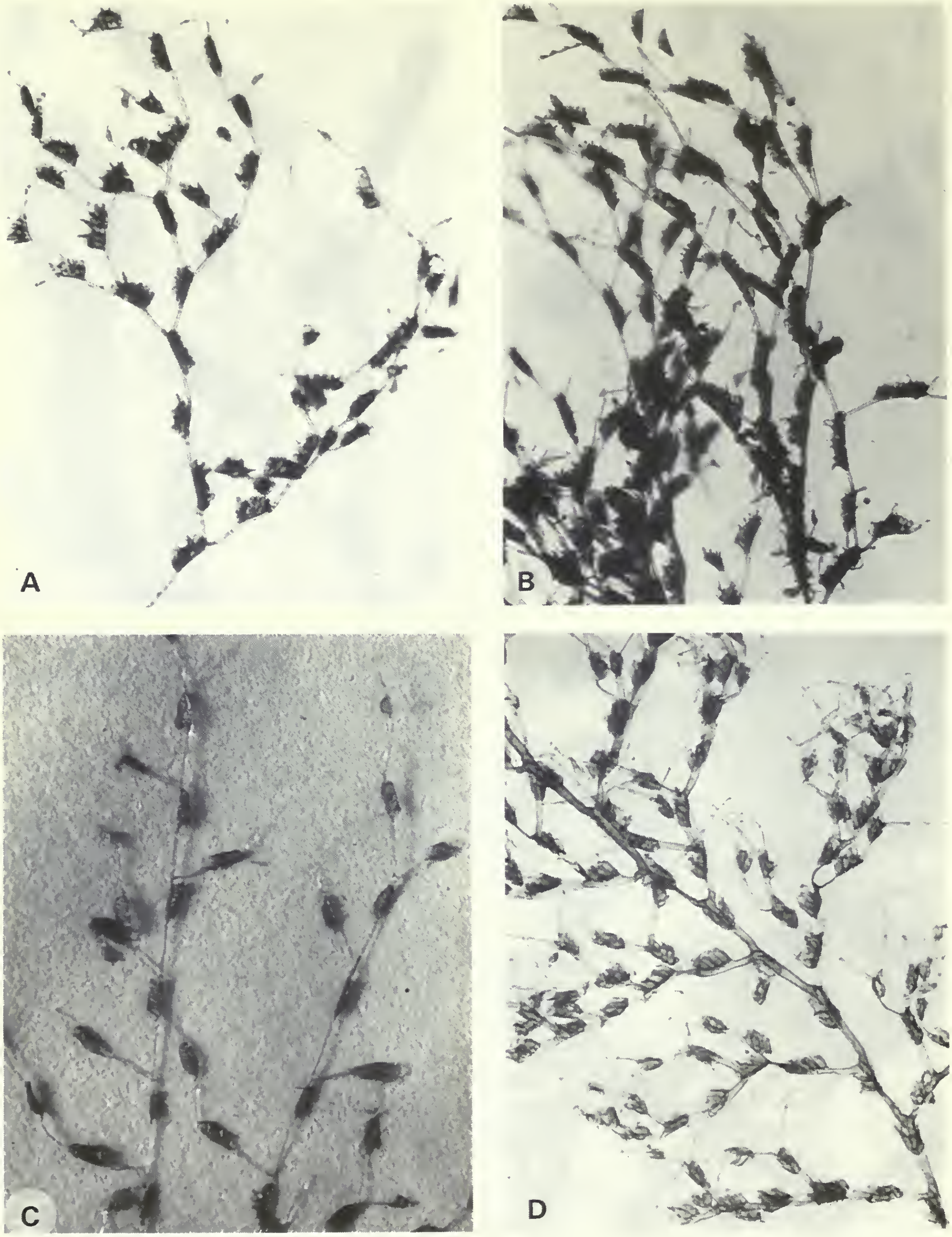

Fig. 7 (A.) *A. lendigera* BMNH 1942.8.6.15, Neotype, Chichester Harbour, UK × 8; (B.) *A. guernseii* BMNH 1898.5.17.189, Holotype, Guernsey, UK × 8; (C.) *A. intermedis* BMNH 1842.12.9.14, Belfast Bay, N. Ireland × 6; (D.) *A. populea* BMNH 1899.7.1.526, Lectotype, Natal, South Africa × 8.

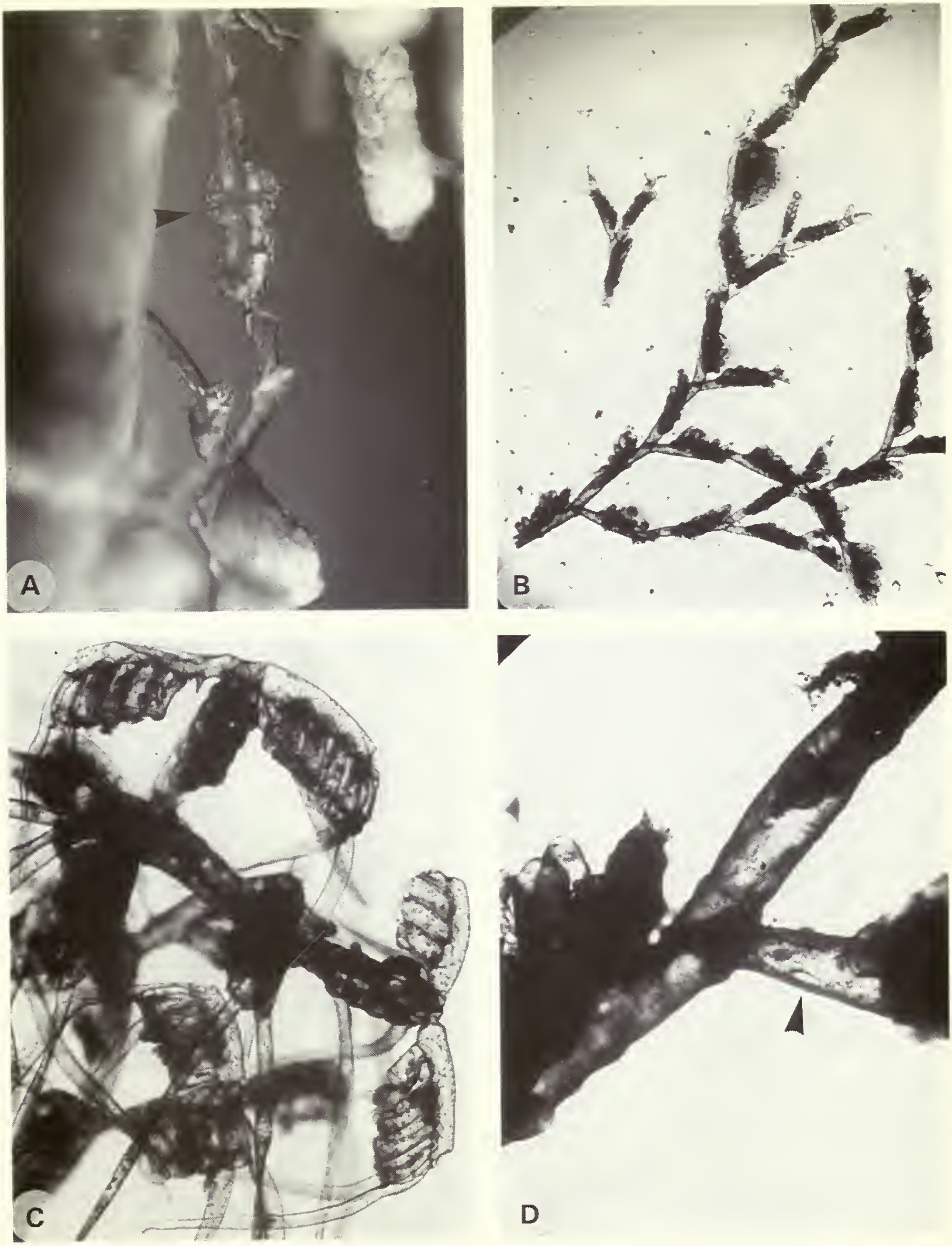

Fig. 8 (A.) *A. lendigera* BMNH 1942.8.6.15, Neotype, Chichester Harbour, UK, palmate processes × 28; (B.) *A. obliqua* NMV H493 (65391) Syntype, Port Phillip Heads, Aus. × 10; (C.) *A. lamourouxi* BMNH 1887.12.10.70, Neotype, Port Phillip, Aus. × 20; (D.) *A. obliqua* NMV H493 (65391) Syntype, Port Phillip Heads, Aus., site of rhizoid origin arrowed × 57.

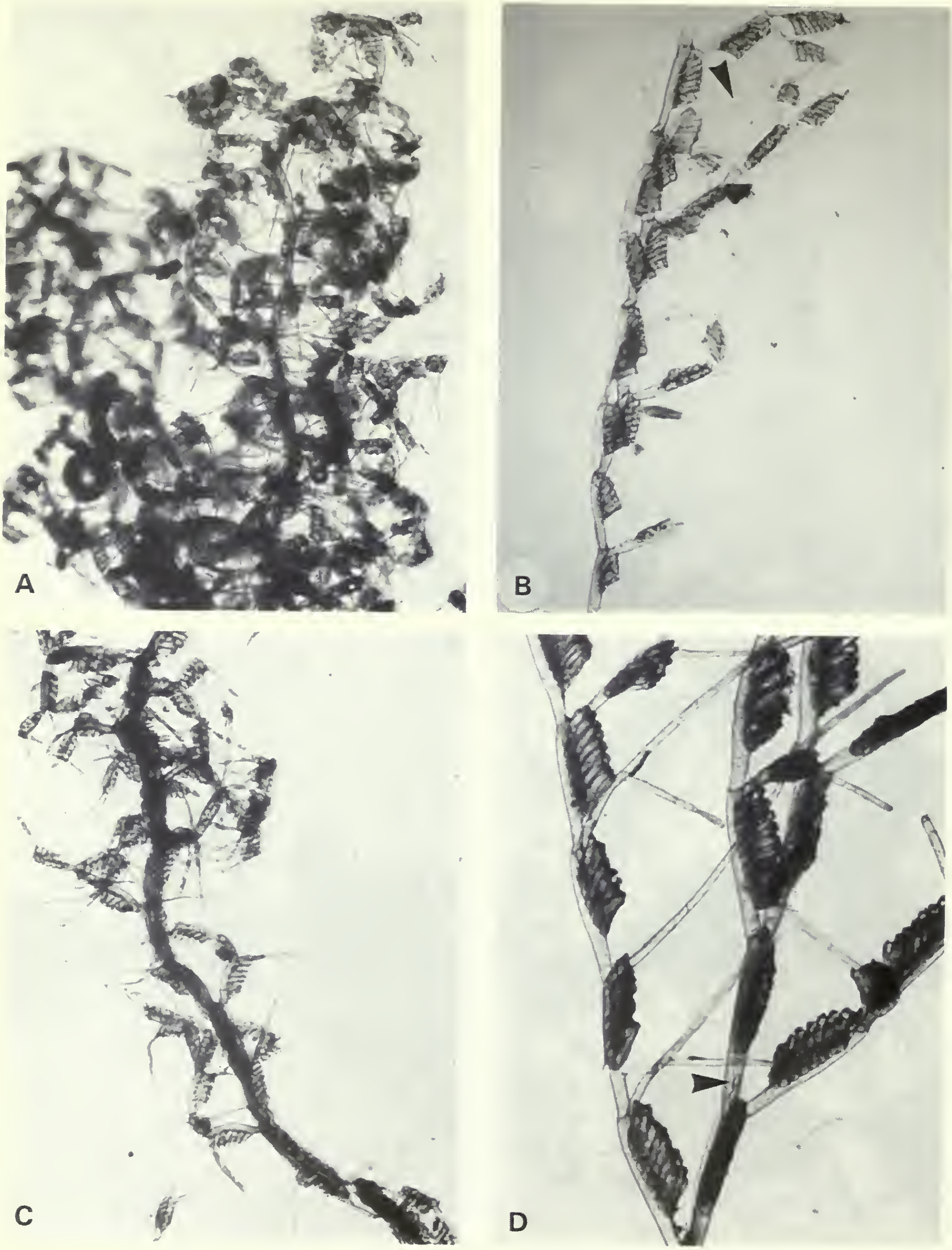

Fig. 9 (A.) *A. lamourouxi* BMNH 1887.12.10.70, Neotype, Port Phillip, Aus. × 8; (B.) *A. cornuta* sensu d'Hondt (*A. woodsii*) LBIMM 2821 part, 'l'Ocean asiatique', bifurcate terminal process arrowed × 8; (C.) *A. lamourouxi* BMNH 1899.7.1.3, New Zealand, apparent alternate branching × 7; (D.) *A. woodsii* BMNH 1883.11.29.27, Neotype, Port Jackson, Aus., rhizoid origin arrowed × 13.

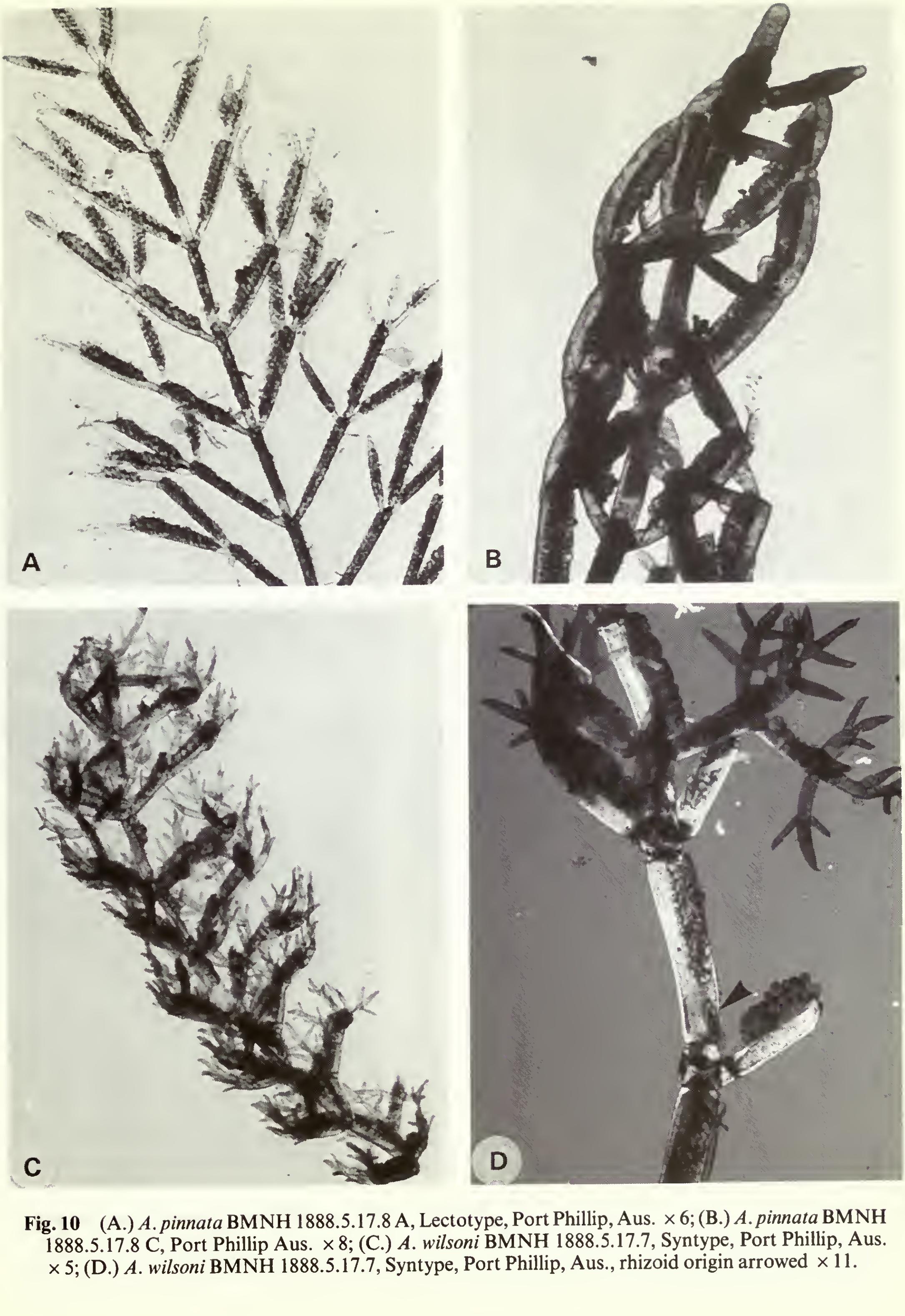

Fig. 10 (A.) *A. pinnata* BMNH 1888.5.17.8 A, Lectotype, Port Phillip, Aus. × 6; (B.) *A. pinnata* BMNH 1888.5.17.8 C, Port Phillip Aus. × 8; (C.) *A. wilsoni* BMNH 1888.5.17.7, Syntype, Port Phillip, Aus. × 5; (D.) *A. wilsoni* BMNH 1888.5.17.7, Syntype, Port Phillip, Aus., rhizoid origin arrowed × 11.

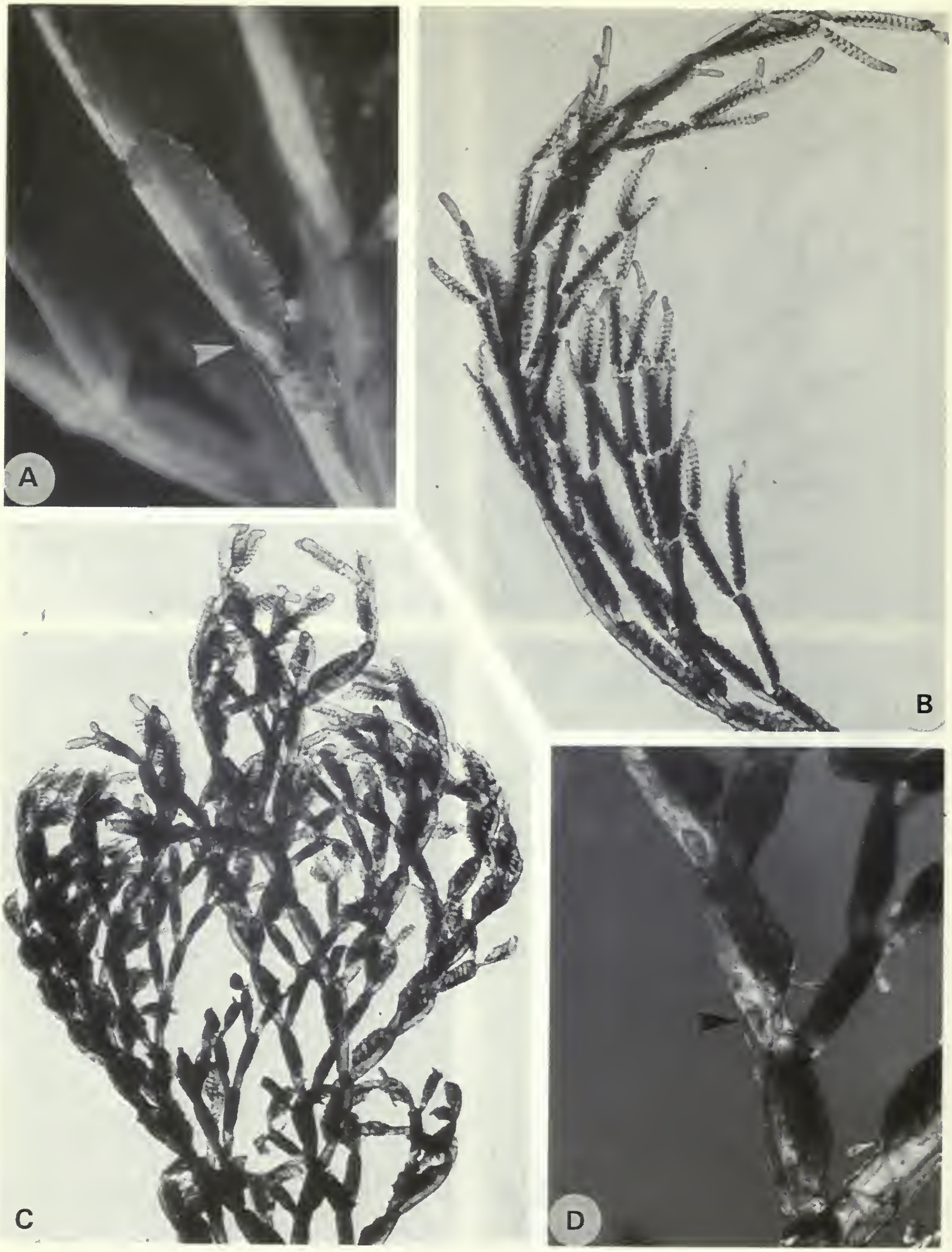

Fig. 11 (A.) *A. brongniartii* BMNH 1888.5.17.6, Neotype, Port Phillip, Aus., rhizoid origin arrowed ×20; (B.) *A. brongniartii* BMNH 1888.5.17.6, Neotype, Port Phillip, Aus. ×8; (C.) *A. biseriata* BMNH 1887.12.10.90, Neotype, Port Phillip, Aus. ×8; (D.) *A. biseriata* BMNH 1887.12.10.90, Neotype, Port Phillip, Aus., rhizoid origin arrowed ×20.

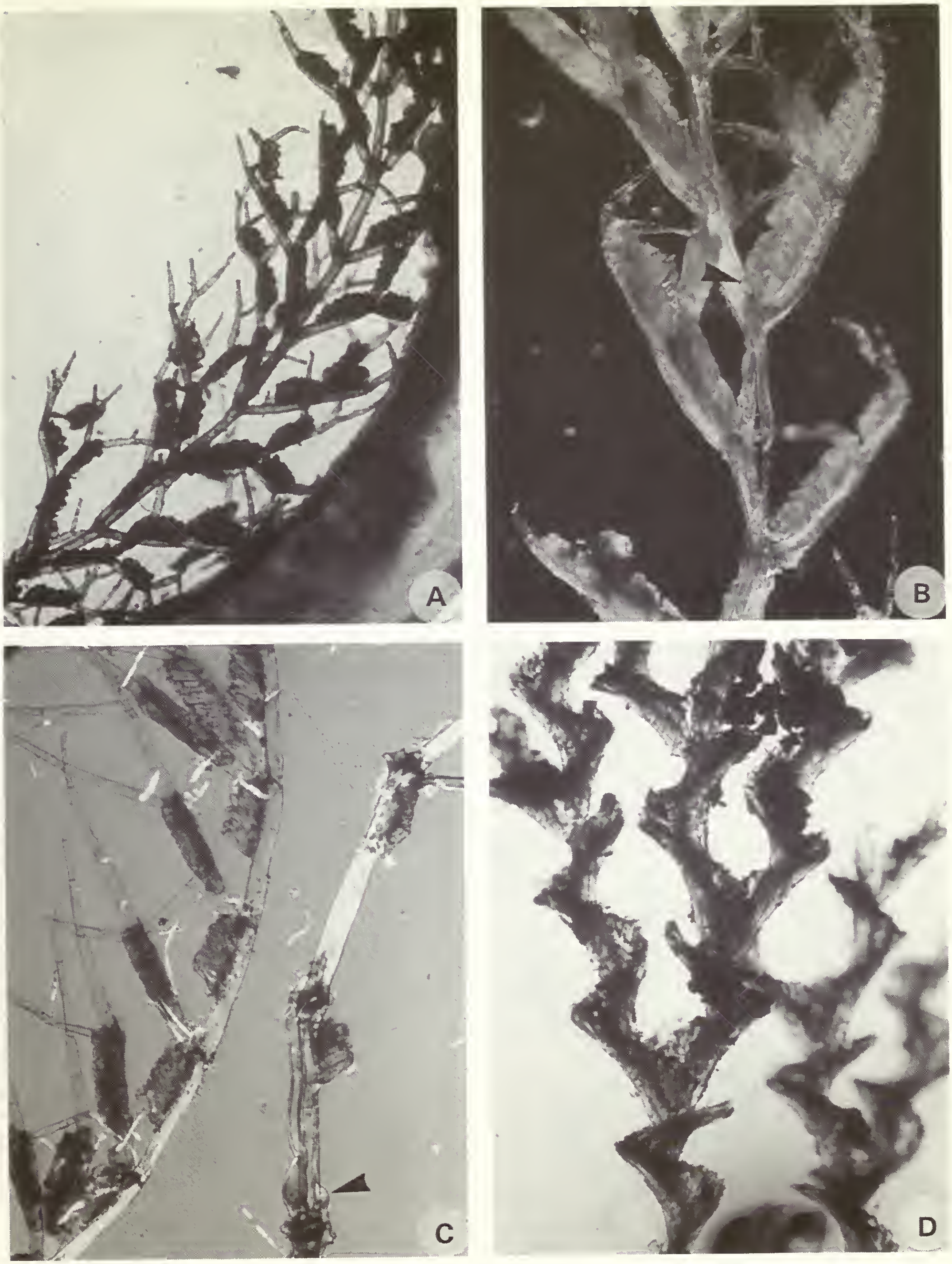

Fig. 12 (A.) *A. plumosa* NMV H494, Holotype, Port Phillip Heads, Aus. × 10; (B.) *A. plumosa* BMNH 1963.2.12.354, Western Australia, rhizoid origin arrowed × 18; (C.) *A. tricornis* BMNH 1899.7.1.6600, Holotype, Australia, rhizoid origin arrowed × 14; (D.) *A. convoluta* (*A. crispa*) BMNH 1899.7.1.6607, Australasia × 10.

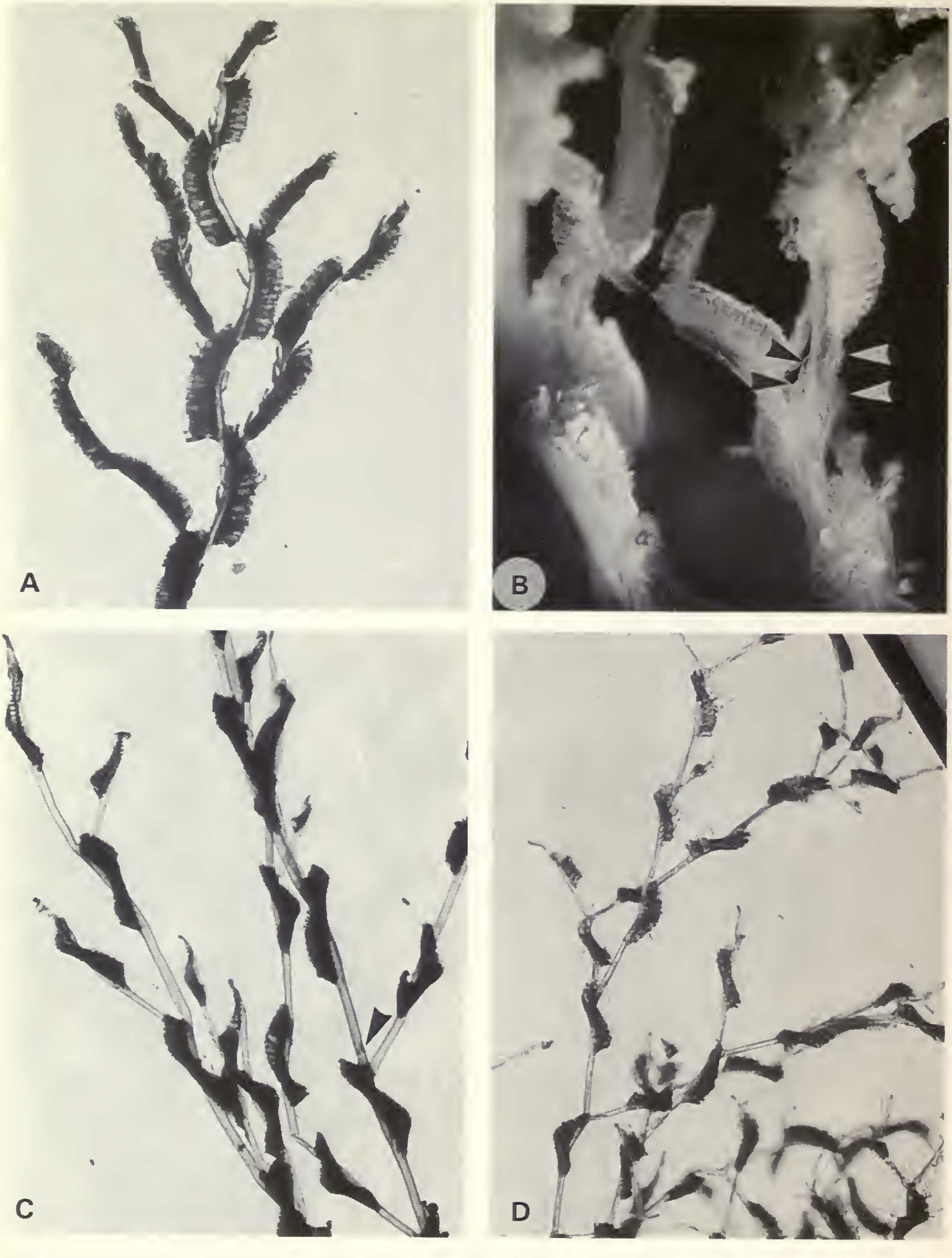

Fig. 13 (A.) *A. alternata* USNM 6307, Neotype, Cape Fear, N.C. USA ×4 (B.) *A. alternata* BMNH 1964.7.10.1A, New River Inlet, N.C., USA, showing polyrhizoid condition, the rhizoid origins indicated × 10; (C.) *A. semiconvoluta* BMNH 1912.12.21.687, Adriatic, rhizoid origin arrowed × 6; (D.) *A. pruvoti* LBIMM Bry 8205, Type × 8.

British Museum (Natural History)

The birds of Mount Nimba, Liberia

Peter R. Colston & Kai Curry-Lindahl

For evolution and speciation of animals Mount Nimba in Liberia, Guinea and the Ivory Coast is a key area in Africa representing for biologists what the Abu Simbel site in Egypt signified for archaeologists. No less than about 200 species of animals are endemic to Mount Nimba. Yet, this mountain massif, entirely located within the rain-forest biome, is rapidly being destroyed by human exploitation.

This book is the first major work on the birds of Mount Nimba and surrounding lowland rain-forests. During 20 years (1962–1982) of research at the Nimba Research Laboratory in Grassfield (Liberia), located at the foot of Mount Nimba, scientists from three continents have studied the birds. In this way Mount Nimba has become the ornithologically most thoroughly explored lowland rain-forest area of Africa.

The book offers a comprehensive synthesis of information on the avifauna of Mount Nimba and its ecological setting. During the 20 years period of biological investigations at Nimba this in 1962 intact area was gradually opened up by man with far-reaching environmental consequences for the rain-forest habitats and profound effects on the birds. Therefore, the book provides not only a source of reference material on the systematics, physiology, ecology and biology of the birds of Mount Nimba and the African rain-forest, but also data on biogeography in the African context as well as conservation problems. Also behaviour and migration are discussed. At Nimba a number of migrants from Europe and/or Asia meet Afrotropical migratory and sedentary birds.

Professor Kai Curry-Lindahl has served as Chairman of the Nimba Research Laboratory and Committee since its inception in 1962. Peter Colston is from the Subdepartment of Ornithology, British Museum (Natural History), Tring, and Malcolm Coe is from the Animal Ecology Research Group, Department of Zoology, Oxford.

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